



**Molecular Characterization and Genome-Wide Association Mapping
for Root System Architecture and Quality Related Traits in
Ethiopian Durum Wheat (*Triticum turgidum* ssp. *durum*) with High
Density SNP Markers**

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Addis Ababa, Ethiopia
December, 2019**



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Density SNP Markers**

**A Thesis Submitted to the Department of Microbial, Cellular and Molecular
Biology, Addis Ababa University, in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy in Biology (Applied Genetics)**

By

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December 2019

Declaration

I, the undersigned, declare that this dissertation is entirely my original work and its composition has never been submitted elsewhere for any other awards. All assistance towards the synthesis of this thesis and entire references of others contained herein have been duly acknowledged.

Name: Admas Alemu **Signature:** _____ **Date:** _____

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ACRONYMS AND ABBREVIATIONS

AM	Association Mapping
AMOVA	Analysis of molecular variance
ANOVA	Analysis of variance
ARL	Average Root Length
CIE	International Commission on Illumination
CIE a*	Redness
CIE b*	Yellowness
CIE L*	Brightness
cM	Centi Morgan
CWANA	Central and West Asia and North Africa
CSA	Ethiopian Central Statistical Agency
DZARC	Debre Zeit Agricultural Research Center
FAO	Food and Agriculture Organization
GAIN	Global Agricultural Information Network
GL	Grain Length
GLM	General Linear Model
GW	Grain Width
GWAS	Genome-Wide Association Study
IRW	Individual Root Weight
iTGW	initial Thousand Grain Weight
K	Kinship similarity
LD	Linkage Disequilibrium
MAF	Minor Allelic Frequency
MLM	Mixed Linear Model
MTA	Marker Trait Association
PCA	Principal Component Analysis
PIC	Polymorphic Information Content
Q	Population Structure
QTL	Quantitative Trait Loci
RDW	Root Dry Weight
RGA	Root Growth Angle
RSA	Root System Architecture

RSR	Root Shoot Ratio
RT6	Presence of 6 th Seminal Root
SARC	Sinana Agricultural Research Center
SDW	Shoot Dry Weight
SNP	Single Nucleotide Polymorphism
SSA	Sub-Saharan Africa
TASSEL	Trait Analysis by ASSociation, Evolution and Linkage
TGW	Thousand Grain Weight
TRL	Total Root Length
TRN	Total Root Number
YPC	Yellow Pigment Content

ABSTRACT

Molecular Characterization and Genome-Wide Association Mapping for Root System Architecture and Quality Related Traits in Ethiopian Durum Wheat (*Triticum turgidum* ssp. *durum*) with High Density SNP Markers

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Addis Ababa University, December 2019

Durum wheat is an allotetraploid wheat ($2n = 4x = 28$, AABB) commonly used for production of semolina (purified flour of durum wheat mainly used in making pasta and couscous) worldwide. Durum wheat is indigenous to Ethiopia and farmers have grown the crop since immemorial time, mostly under adverse environmental conditions and developed a broad gene pool adapted to various environmental conditions. Hence, dissecting and identifying the genetic basis of agronomically relevant traits have paramount importance to enhance the yield, improve the quality and reduce genetic vulnerability to various stresses. The present study aimed to assess the genetic diversity and map valuable QTLs for root system architecture, grain shape and color related traits through genome-wide association (GWAS) analysis. A total of 192 Ethiopian durum wheat comprising 167 landraces and 25 improved varieties were assembled for this study. High-density Infinium® iSelect® Illumina 90K wheat SNP array was used to genotype accessions and 15,338 polymorphic SNPs were generated that was used for genetic diversity analysis. After excluding markers with < 0.05 minor allele frequency and > 0.1 missing values per accession and followed by imputation, 10,789 SNP markers with known chromosome position were used for GWAS analysis of root system architecture, grain shape and color related traits. Linkage disequilibrium, population structure and kinship of the panel were also estimated based on LD-pruned SNP markers. Mean values of Nei's gene diversity (0.246) and polymorphic information content (0.203) specified the presence of rich genetic diversity within this collection. Varieties grouped in a distinct cluster separately from landraces in clustering analysis and landraces clustering was irrespective of their geographical origin, signifying the presence of higher admixture that could arise due to the existence of historical exchange of seeds through informal seed exchanging systems involving regional and countrywide farming communities.

Four major and 34 nominal QTLs were identified for ten RSA traits making one clear root growth angle cluster on the chromosome arm 6AL and 15 clusters for the rest of RSA traits across chromosomes. After mapping the identified QTLs on a high-density tetraploid consensus map along with previously reported RSA QTLs in durum and bread wheat, fourteen nominal QTLs were found to be novel. Two novel major QTLs along with 18 nominal QTLs were detected for kernel length, width and color-related traits. The current high-density SNP based genetic diversity and QTL mapping analysis proved the presence of rich genetic variation and source of novel alleles in Ethiopian durum wheat. Hence, sustainable utilization and conservation of this rich durum wheat genetic resource is incomparable to cope up the recurrent climate changes and biotic stresses. Identified QTLs and chromosome regions of RSA and quality-related traits could be used as a tool to employ marker-assisted selection aimed to enhance yield, yield stability and quality of durum wheat. Further investigations including validation, fine mapping and positional cloning of major and novel RSA and quality-related QTLs identified in the current study is highly recommended to employ MAS or genomic editing to enhance durum wheat breeding.

Keywords: Ethiopian durum wheat, GWAS, QTLome, Genetic Diversity, SNPs, RSA, Grain color, Shape.

1. INTRODUCTION

1.1. Background and Justification

Modern wheat varieties generally refer to two species: hexaploid bread wheat, *Triticum aestivum* ($2n = 6x = 42$, AABBDD), and tetraploid/hard or durum wheat, *T. durum* ($2n = 4x = 28$, AABB) used for pasta, macaroni, couscous and low-rising bread, and the former accounts for about 95% of world wheat production and durum covers the other 5% (Peng *et al.*, 2011).

In Ethiopia, wheat is the second most widely produced cereal crop after corn and third most important staple food after corn and sorghum (GAIN, 2018). Hard white bread wheat accounts for about 85-90 percent of production, while durum makes up roughly 10-15 percent (GAIN, 2018). Wheat has versatile uses in making various foods and drinks, such as bread, ‘Kolo’ (traditional Ethiopian snack made from wheat mixed with barley, chickpea and other legumes and roasted in a clay griddle), ‘Tella’ (traditional Ethiopian beer), pasta, macaroni, biscuits, cakes, sandwich, and others. Additionally, wheat straw has been commonly used as a roof thatching material and as animal feed in most wheat-growing rural areas of Ethiopia.

Durum wheat production has gradually increased globally since the 1950s. However, as the world population is predicted to rise to 9.1 billion by 2050 (FAO, 2015), which is 34% higher than the current population size, breeding cereals, including durum wheat, with improved yield and quality performance has become urgent and relevant. Increasing wheat production is the primary national goal in Ethiopia in order to decrease the gap between production and human consumption especially due to the

higher level of annual puplation growth rate as compared to the annual rate of wheat production increament.. Demand for durum wheat has steadily increased in the last decades in Ethiopia particularly due to the emergence of many food processing industries. Meanwhile, durum productivity has been curtailed by many abiotic and biotic sresses.

Ethiopia is a food-insecure developing country in which agriculture provides the basis of the economy. Ethiopia's crop genetic resources is in contrast to the existing food insecurity of the nation. Many previous findings reported the presence of high genetic diversity of cultivated durum wheat and this is due to wide range of agro-ecological conditions coupled with diverse farmers' culture. Vavilov (1951) and Zohary (1970) reported the presence of high genetic diversity in cultivated tetraploid wheat and considered Ethiopia to be a center of diversity and the site of origin for tetraploid wheat. Ethiopian farmers have grown durum wheat since immemorial time, mostly under adverse environmental conditions. They developed a broad gene pool of durum wheat landraces adapted to various environmental conditions. However, in recent times durum wheat has been dominated and replaced by bread wheat in the country particularly due to lack of improved durum wheat varieties with resistance rust diseases (Negassa *et al.*, 2012).

Ethiopian durum wheat landraces provide a huge and yet untapped biodiversity. Previous genetic diversity studies carried out with phenotypic (Bechere *et al.*, 1996; Tesemma and Bechere, 1998; Teklu and Hammer, 2008; Mengistu *et al.*, 2015) and molecular approaches (Alamerew *et al.*, 2004; Teklu *et al.*, 2006; Haile *et al.*, 2013; Mengistu *et al.*, 2016) have shown high level of genetic diversity and also unique

sources of useful traits (Amri *et al.*, 1990; Kubo *et al.*, 2004, Liu *et al.*, 2017). Dissecting and identifying the genetic basis of agronomically relevant traits from the existing durum wheat gene pool have paramount importance in order to enhance the yield, improve the quality and reduce genetic vulnerability to various abiotic and biotic stresses. In this regard, hardly any work has been carried out previously.

Ethiopia is known for the recurrence of drought, as shown by the devastating drought occurred in 2015/16 caused severe damage and loss to crops. Recent evidence suggests that the incidence of droughts in Ethiopia has increased in the last ten years relative to the decade before (Mann and Warner, 2017). Therefore, improving crop adaptation to water- and nutrient-limited environments has been a major breeding target.

Roots are important to plants for a wide variety of processes, including nutrient and water uptake, anchoring and mechanical support, storage functions, and as the major interface between the plant and various biotic and abiotic factors in the soil environment. The root system architecture (RSA) describes the shape and structure of the root system, both of which have great functional importance. The shape defines the distribution of the roots in space and the way the root system occupies the soil. The root shape can be described through several geometrical criteria, as the lateral root extension or the root depth, or in more detail, as the distribution of the root length density in the soil. The root structure refers to the diversity of their components or root segments and their relationships (Canè *et al.*, 2014).

RSA plays a crucial role in crop performance, particularly for cultivations under non-optimal nutritional and water supply conditions (de Dorlodot *et al.*, 2007; Lynch and Wojciechowski, 2015). Enhancing the genetic capacity of roots that enables to capture soil resources is considered a primary target for breeding in modern crops (Reynold and Tuberosa, 2008; Hawkesford *et al.*, 2014; Mickelbart *et al.*, 2015). Selecting wheat with an improved capacity to maintain root growth under drought conditions would result in increased yield and yield stability under water-limited environments (Wasson *et al.*, 2012, 2014; Christopher *et al.*, 2013). The identification of quantitative trait loci (QTL) for RSA traits provides wheat breeders with indirect selection targets for root growth pattern and/or adaptation to drought stress conditions (Blum, 2009; Nakhforoosh *et al.*, 2015; Pinto *et al.*, 2015). In rice, the identification of a major QTL for RSA features (deeper rooting 1, DRO1) has allowed for the exploitation of the beneficial allele through marker assisted selection while allowing for the positional cloning of the causative locus (Uga *et al.*, 2013).

Today, the other challenging task for durum wheat breeders is not only to increase grain yield but also to improve the grain quality for end products to meet the requirement of the rapidly increasing population in the world. Quality refers to the desirability of the product and may include various physical and chemical aspects depending on the intended purpose. The durum wheat grain quality traits are considered to be inherited as quantitative traits (QTLs) as it is known to be controlled by a group of genes and being affected by environmental variations. The quality of end product is related to the quality of the durum grain, which is mainly determined by the genotype, but also by the environment. Quality improvement in durum wheat is possible through evaluation and selection, from the existing wide variations in the

breeding material (Peterson *et al.*, 1998). The genetic progress that can be achieved through breeding is largely dependent on the identification of genotypes with better quality attributes and of critical traits on which selection can be based (Ammar *et al.*, 2000). Due to its superior characteristics, durum wheat is primarily used for the production of high-quality semolina, pasta, or macaroni products. This is mainly because of its higher level of yellow pigments and protein as well as superior gluten characteristics (Troccoli *et al.*, 2000). In addition, kernel size, shape and vitreousness plays greatest importance in durum wheat quality, as they are strongly related to semolina yield, bright yellow appearance of semolina, and cooking properties of pasta products (Troccoli *et al.*, 2000; Dziki and Laskowski, 2005).

In the past couples of decades, increasing efforts have been devoted to genomics-assisted breeding as a complement to conventional pedigree-based selection, with an emphasis on QTL identification and marker-assisted selection (MAS). Marker-assisted selection allows breeders to select for beneficial traits that are either difficult to measure and/or have low heritability and are expressed late in development, hence impairing an accurate assessment of the genetic potential of specific genotypes prior to phenotypic evaluation. The genetic sources of phenotypic variation have been a major focus in many crop plant studies aimed at identifying the causes of many agronomically relevant traits. Traditionally, QTLs were used to map in different crops using bi-parental crosses, which is restricted in a very small allelic diversity and having limited genomic resolution. Genome-wide association study (GWAS) approach overcomes several limitations over QTL linkage-based mapping by providing higher resolution and using samples from previously well-studied populations in which commonly occurring genetic variations can be associated with

phenotypic variation. GWAS is a strong statistical tool that includes genotyping a large collection of accessions with tens or hundreds of thousands of SNPs through the whole genome and conduct association analysis with phenotypic trait(s) of interest (Andreas and Christensen, 2016). GWAS involves testing for association in most of the segments of the genome by genotyping densely distributed genetic marker loci covering all chromosomes. GWAS mapping enables us to screen a huge number of accessions for genetic variation underlying diverse complex traits (Atwell *et al.*, 2010; Maccaferri *et al.*, 2011). The introduction of high-density single nucleotide polymorphism (SNP) typing (Wang *et al.*, 2014) allowed whole genome scans to identify small haplotype blocks that are significantly correlated with quantitative trait variation (Maccaferri *et al.*, 2016). This approach has been successful in identifying loci that explain large portions of phenotypic variation (Atwell *et al.*, 2010; Canè *et al.*, 2014; Maccaferri *et al.*, 2016).

Hybridization arrays/microarrays have been used as a preeminent solution to develop single nucleotide polymorphisms (SNPs) in complex polyploid genomes such as wheat (Wang *et al.*, 2014). The technology avoids the risk of miscalling diversity on homoeologous genomes and its power recently increased 10-fold in wheat moving from 9K to 90K genome-wide SNPs (Mengistu *et al.*, 2016).

This PhD dissertation research aimed to conduct genetic diversity analysis and detect QTLs for root system architecture, grain shape and color-related traits with GWAS analysis in Ethiopian durum wheat accessions to disclose the existing genetic variation and spot chromosome regions valuable for future marker-assisted selection or genome editing aimed in enhancing durum production.

1.2. Objectives

General Objective

- ❖ To assess the genetic diversity and map QTLs for root system architecture and quality-related traits through GWAS analysis in Ethiopian durum wheat accessions using high-density SNP markers.

Specific Objectives

- ❖ To evaluate the nature and extent of genetic diversity of Ethiopian durum wheat landraces and varieties using high density SNP markers;
- ❖ To estimate population structure and linkage disequilibrium of Ethiopian durum wheat using high-density SNP markers;
- ❖ To identify quantitative trait loci (QTLs) associated with root system architecture (RSA) traits in Ethiopian durum wheat accessions;
- ❖ To identify quantitative trait loci (QTLs) linked with grain color traits in Ethiopian durum wheat accessions;
- ❖ To detect quantitative trait loci (QTLs) linked with grain shape traits in Ethiopian durum wheat landraces and varieties

2. LITERATURE REVIEW

2.1. Origin, Evolution and Genome of Wheat

Wheat belongs to the Gramineae (Poaceae) family, Triticeae tribe, Triticinae sub-tribe that comprises around 300 species (Matsuoka, 2011). The tribe Triticeae contains three of the major cereals (wheat, rye and barley) being used by humankind since prehistoric times, as well as the first and unique man made cereal called triticale. Triticale is a man made crop which could be Octoploid ($2n = 8x = 56$, AABBDDRR) or hexaploid ($2n = 6x = 42$, AABBRR) triticale are developed by crossing hexaploid wheat and rye ($2n = 6x = 42$, (AABBDD) $\times$ $2n = 2x = 14$, (RR)) or and tetraploid wheat and rye ($2n = 4x = 28$, (AABB) $\times$ $2n = 2x = 14$, (RR), respectively) (Gregory, 1987).

Wheat is one of the oldest crops, as established from abundant archaeological, religious (e.g. Biblical stories) and historical evidence indicating its importance to human civilization (Fuller, 2007). Wheat domestication occurred around 10,000 years ago when humans started to shift from hunting and gathering to crop production (Shewry, 2009). Wheat to get its present-day form has gone through a long and interesting evolution. The origin of the genus *Triticum* is in the area that is known as the Fertile Crescent and parts of Africa covering the area stretching from Syria to Kashmir, and southwards to Ethiopia (Dubčovský and Dvořák, 2007).

Wheat is a classic example of how closely related species may be combined in nature into a polyploid series. Wheat species can be divided into diploid, tetraploid, and hexaploid groups, with chromosome numbers of $2n = 14$ (2x), 28 (4x), and 42

(6x), respectively, in which the basic chromosome number is $x = 7$. From the rich variety of wheat species and forms, bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* var. *durum*) are important for human diet (Peng *et al.*, 2011). Bread and durum wheat are allohexaploid and allotetraploid species with a large genome size with 16 and 11 Gb, respectively (Ganal and Röder, 2007; Mayer *et al.*, 2014).

Wheat species represent an allopolyploid series ($x = 7$) based on genomes A, B, D, and G. The wild species are diploids, ($2n = 2x = 14$), with the genome designation AA (*Triticum monococcum* or *Triticum urartu*), BB (*Aegilops speltoides*), DD (*Triticum tauschii*, syn. *Aegilops squarrosa*), and SS (*Triticum speltoides*). While cultivated species are allotetraploids ($2n = 4x = 28$ chromosomes) with genomic formula AABB (*Triticum dicoccoides*, *Triticum dicoccum*, and *Triticum turgidum* var. *durum* Desf.) and AAGG (*Triticum timopheevi*) and allohexaploid ($2n = 6x = 42$ chromosomes) with genomic formula AABBDD (*Triticum aestivum* ssp. *spelta* and *Triticum aestivum* ssp. *aestivum*) (Friebe and Gill, 1996; von Buren, 2001; Colomba and Gregorini, 2011).

The wild tetraploids *T. turgidum* ssp. *dicoccoides* arose from hybridization between *T. urartu* or *Triticum monococcum* (A donor) and the putative B donor *Aegilops speltoides*. However, it remains uncertain whether *Ae. speltoides* is the sole source of the B genome or whether the genome resulted from an introgression of several parental species (Zohary and Feldman, 1962). *T. turgidum* (AABB) includes the wild ssp. *dicoccoides* and several cultivated subspecies including *T. turgidum* ssp. *durum*.

Tetraploid wheats are represented by two wild and twelve cultivated species grouped into two evolutionary lines (sections) – Emmer and Timopheevii (Goncharov, 2011; Hammer *et al.*, 2011). At present, only five of them, namely *Triticum durum* Desf., *T. turgidum* L., *T. dicoccum* (Schrank) Schuebl., *T. aethiopicum* Jakubz. and *T. turanicum* Udazch. are cultivated. Durum wheat, *Triticum turgidum* var. *durum*, is a tetraploid species whose genome is genetically very close to that of its progenitor, wild emmer wheat, *Triticum turgidum* ssp. *dicoccoides* ($2n = 4x = 28$, genome AABB) (Feldman, 2001). From the wealth of varieties and forms of domesticated emmer wheat in Ethiopia, as compared with the relatively few variations in other areas of the globe, Vavilov (1951) assumed Ethiopia to be the site of domestication of tetraploid wheat.

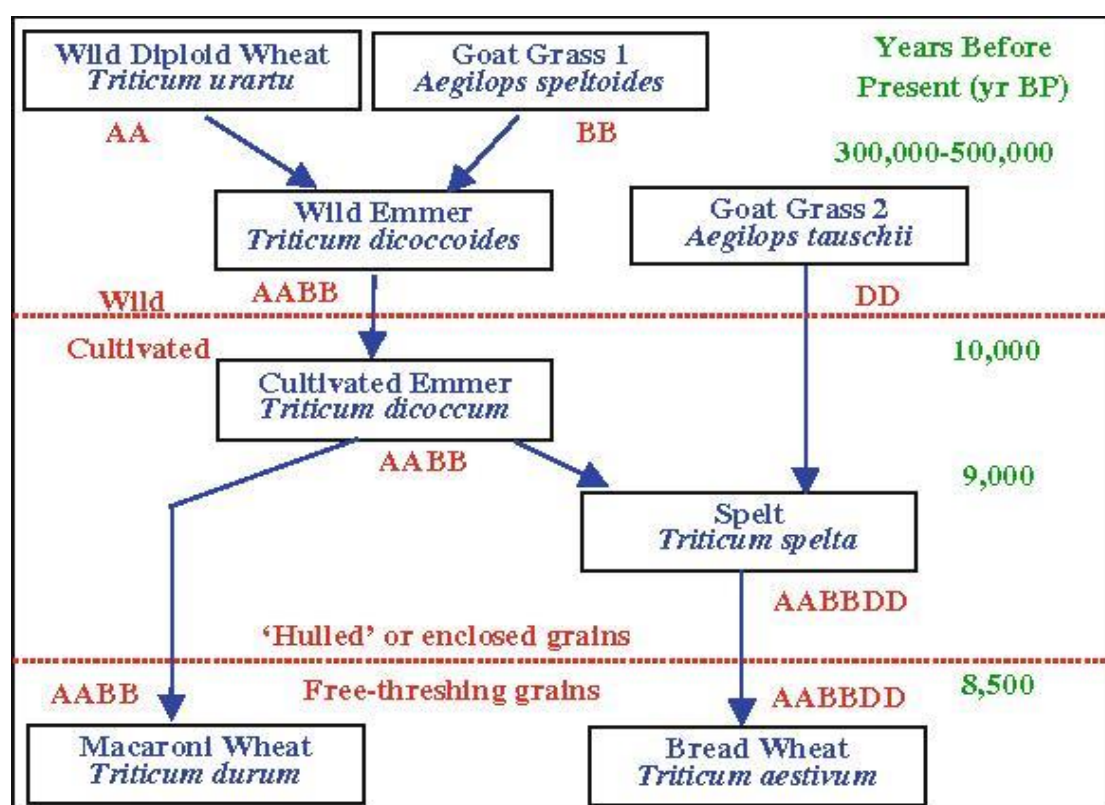


Figure 1. Evolution of wheat from the prehistoric Stone Age grasses to modern durum and bread wheat (reproduced from <http://www.newhallmill.org.uk/wht-evol.htm>).

2.2. Domestication of Durum Wheat

Two major steps were involved during durum wheat domestication (Feldman, 2001). The first step was the domestication of wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*) with the loss of fragility of spikes (disarticulation into spikelets) (Feldman, 2001; Salamini *et al.*, 2002). Genetic and archeological evidences proved that this step was a steady process and two to three major loci and numerous modifiers with additive effects controlled fragility and took longer time to fix the mutations for the loss of fragility (Chen *et al.*, 1998; Watanabe *et al.*, 2002; Nalam *et al.*, 2006; Millet *et al.*, 2013). The complete loss of fragility gave rise to the first domesticated wheat called emmer wheat (*Triticum turgidum* ssp. *dicoccum*). Emmer wheat is still cultivated in many countries in small scale (De Vita *et al.*, 2006). Despite its spike is non-fragile, like its progenitor, emmer wheat has only two kernels per spikelet which is tightly wrapped in stiff glumes and it is not free threshing (De Vita *et al.*, 2006).

The second step was the rise of durum from emmer wheat (i.e. the appearance of naked kernels). Different suggestions have been made for this step (Feldman, 2001). As per the archeological evidences, even though durum-like wheat has appeared around 7000 BP, durum was a major crop only around 3000 years ago probably because of its susceptibility to diseases. On the other hand, a tetraploid fossil wheat species, *Triticum turgidum* ssp. *parvicoccum*, was relatively abundant in the archeological record starting already 9000 years BP, but disappeared ~ 2000 years BP. This species had a compact spike and was free trashing suggesting that it probably already contained the mutations of genes that control glume stiffness (Q factor and the *Tenacious Glumes* (TG) locus) (Feldman and Kisslev, 2007). This

raises the possibility that durum has these mutations from *parvicoccum*, rather than evolving them independently from emmer wheat. Durum may thus have derived from hybridization between *parvicoccum* and *dicoccum* receiving the free-threshing trait from *parvicoccum* and the large grains from *dicoccum* but the preference of large grain of durum than the smaller found in *parvicoccum* leads the prominence of durum as a tetraploid wheat and to the extinction of *parvicoccum* (Ben-Abu *et al.*, 2014).

In addition, many domestication traits had passed a selection process that were advantageous to farmers, such as plant erectness versus the wild grassy types, increased number of seeds per spikelet, and reduced seed dormancy (Feldman, 2001). Various QTLs that are not easily detectable with eye were most likely involved in selection process. This included QTLs related with resistance to abiotic and biotic stresses, physiological parameters that contribute to yield (Peleg *et al.*, 2009), as well as quality parameters (Levy and Feldman, 1989) and in recent decades, following the green revolution, adaptation to the new cultivation conditions including chemical fertilizers and mechanical harvest (Ben-Abu *et al.*, 2014). The Q locus, located on chromosome 5A, is the only domestication related locus characterized so far at the molecular level. It is one of the most significant domestication loci as it controls spike compactness, glume tenacity and fragility and it encodes for the APETALA2-like transcription factor (Simons *et al.*, 2006). While the 5A homeoallele has the most significant contribution, other homeoalleles were also shown to be involved in the domestication traits (Zhang *et al.*, 2011). So far, other domestication related QTLs/genes have been characterized only through genetic mapping. The two major genes that control spike fragility (*Brittle Rachis 2* and *Brittle Rachis 3*) are located on the short arms of chromosomes 3A and 3B, respectively (Nalam *et al.*, 2006). Another

locus controlling spike delicateness also is mapped on chromosome 2A (Peng *et al.*, 2003; Peleg *et al.*, 2011). Storage proteins, in particular the high molecular weight (HMV) glutenins whose variability and amounts are higher in wild than in domesticated durum, are among the traits that were highly affected through domestication of durum wheat (Laido *et al.*, 2013; Levy and Feldman, 1988).

2.3. Wheat Distribution and Production in Ethiopia

Ethiopia is the second largest wheat producer in Sub-Saharan Africa next to South Africa (FAO, 2015). Wheat is one of the major cereal crops in the country and it is grown between 6 and 14° N latitudes and 35 and 42° E longitude ranging in altitude from 1500 to 3200 masl but the most suitable regions fall between 1900 and 2700 masl (Hailu, 1991). In Ethiopia, the rainy season is divided into the short rains (belg) falling from February to April and the main rains (meher) falling from June to September. Wheat is produced solely under rainfed conditions and from the total wheat production, it has been reported that tetraploid and hexaploid species have shared approximately 50% of the area (Gorfu *et al.*, 2001) in the past. However, in recent years, durum wheat has been surpassed by bread wheat occupying approximately 20 and 80%, respectively, of the total wheat area under cultivation (Negassa *et al.*, 2012; GAIN, 2018). With a lesser extent, other wheat species are also cultivated in the country. For instance, Ethiopia is one of the very few countries where emmer wheat is still under cultivation and other species like *Triticum polonicum* and *Triticum aethiopicum* are also grown in mixtures with other wheat species (Eticha *et al.*, 2005).

In Ethiopia, durum wheat is commonly planted on heavy black clay soils (vertisols)

of the highlands between 1800 and 2800 masl (Tesemma and Belay, 1991). Bozzini (1988) reported that durum wheat is best adapted to regions having a relatively dry climate, with hot days and cool nights during the growing season, typical of Mediterranean and temperate climates. The majority of durum varieties in Ethiopia are landraces that are often highly admixed (Eticha *et al.*, 2005). Ethiopian farmers traditionally grow several varietal mixtures in the same field that might have advantage to add variety to their diet, reduce the risk of pests and diseases or unusual environmental conditions, and continued to grow traditional even less productive varieties and wild relatives, and, therefore, preserve varieties and genetic diversity (Bekele, 1984; Jain, 2000).

Wheat consumption in Ethiopia has risen faster than any other major food grain, especially for pasta and bread consumption, and is expected to continue to rise rapidly in the future. While the rising demand for pasta in Ethiopia is largely satisfied by the domestic pasta industry, the growing demand for durum wheat that results is largely met through imports. Ethiopia's increasing reliance on food imports from volatile global markets has raised concerns over national food security, as has the possibility that imports may negatively affect the livelihoods of small-scale farmers (Biggeri *et al.*, 2018). The demand of wheat far exceeds the local production in Ethiopia and the country imports large amount of wheat annually costing huge amount of money and continued as a burden to foreign currency (Negassa *et al.*, 2012).

Data on the annual production and productivity of durum wheat has not been documented in annual Ethiopian statistical abstracts published by the Ethiopian

Central Statistical Agency (CSA, 2013) and the national annual average yields is still in scanty. However, the yield of improved durum wheat varieties reported by research institutions in the central highland plateau of Ethiopia under researcher-managed conditions was encouraging, although it must not be considered the national average yield (Mengistu *et al.*, 2016).

2.4. Genetic Improvement of Wheat

Plant genetic resources are sources of diversity of genetic material within plants important for agriculture including plant landraces, genetic stock, primitive forms of cultivated species, modern and obsolete varieties, breeding lines, weeds, wild relatives and unrelated species (Hawkes *et al.*, 2000).

World's trend in wheat production has seen a substantial increase during the second half of the 20th century (Evenson and Gollin, 2003). The two basic causes are: an increase in the overall harvested area which occurred mainly in the first half of the century, followed by the rising importance of an increased grain yield which has been attributed both to genetic gain in yield potential and to improved agronomic practices (Slafer *et al.*, 1994). A considerable boost in genetic gains in wheat yield potential has occurred during the so-called 'Green Revolution' with the release of new improved varieties (Borlaug, 1972).

Marker-assisted selection accelerates the variety development process in plant breeding. Several marker systems have been used for QTL mapping of different crop species. Both bi-allelic and multi-allelic co-dominant markers are suitable for estimating linkage disequilibrium. Simple sequence repeats (SSRs) and restriction

fragment length polymorphisms (RFLPs) have been widely used for QTL mapping (Landjeva *et al.*, 2007). Among dominant markers, amplified fragment length polymorphisms (AFLPs) and randomly amplified polymorphic DNAs (RAPDs) have also been used successfully in QTL mapping despite their low statistical power in relation to co-dominant markers (Abdurakhmonov and Abdurkarimov, 2008). More recently, however, Single Nucleotide Polymorphism (SNPs) and Diversity Array Technology (DArT) markers have been widely utilized for genome wide scanning of QTL in many crop plants. The development of sequencing technologies has allowed the discovery of several fold greater numbers of SNPs than DArT markers in many crop species (Poland *et al.*, 2012).

2.5. Association Mapping

Primacy of plant genetics and breeding research community is to increase yield and stability of major crops to ensure food security for the world fast growing population. To encounter this challenge, plant breeding methods, genetic designs, genomics, statistics, and bioinformatics need to be integrated to modify the adaptive, agronomic, and economic characteristics. The two related components of this effort are gene identification and complex trait dissection. While gene identification focuses on individual genes, complex trait dissection emphasizes genetic contribution and modes of action from many loci, called quantitative trait loci (QTL), which leads phenotypic variation. The two common goals of any quantitative trait loci (QTL) mapping in plants are; (1) to increase our biological knowledge of the inheritance and genetic architecture of quantitative traits, both within a species and across related species, and (2) to detect markers that can be used as indirect selection tools in breeding programs (Bernardo, 2008).

In recent time, the major efforts are being carried out to support the traditional phenotypic pedigree based selection systems of plant breeding with molecular genetics tools for QTL identification and application for marker assisted selection (MAS) and Genomic selection (GS). Linkage mapping (also known as genetic mapping) and association mapping (linkage disequilibrium (LD) mapping) are the most commonly used approaches in dissecting complex traits and identifying genes underlying trait variation in plants, animals, and humans (Risch and Merikangas, 1996).

Molecular markers linked to QTL for traits of interest are being routinely developed in many crops, using materials derived from planned crosses such as inbred lines (F₂s), back crosses (BCs), back-cross inbred lines (BILs), recombinant inbred lines (RILs) and others. Many of these markers have been successfully applied in several plant breeding programs (Collard and Mackill, 2008). However, results of MAS based on linkage-based QTL mapping have been modest (Collard and Mackill, 2008; Ruan *et al.*, 2010) because of the following reasons: I) In linkage-based QTL analyses, there is a non-availability of mapping populations or only few genotypes that are used as parents of mapping populations may not be effective in different backgrounds; II) Lack of substantial time needed to develop such mapping populations;; III) Only few genotypes that are used as parents of mapping populations could be screened for marker-trait associations; IV) The success of MAS based on QTL linkage-based mapping analysis largely depends on the extent of genetic linkage between markers and relevant QTL loci but absence of tight linkage is a problem in mostly linkage-based studies and finally V) The existence of QTL x Environment interactions.

In order to overcome the limitations observed in the linkage-based QTL mapping, recently, association-mapping studies have been conducted in different crop plants. Fast progress in the development of genotyping tools, including genome sequencing and high-density single nucleotide polymorphism (SNP), enabled the development of association mapping, the mapping of complex traits and to the subsequent identification of contributing genes (Gupta *et al.*, 2005, Zhu *et al.*, 2008; Ragoussis, 2009; Appleby *et al.*, 2009).

Association mapping has been variously defined and called as “association genetics”, “association studies” or “linkage disequilibrium mapping”, although the latter term is also used to reflect studies detecting associations among loci (Kruglyak, 1999). Association mapping refers to significant association of a molecular marker with a specific phenotypic trait (Gupta *et al.*, 2005). It has been used as a tool to resolve complex trait variation down to the sequence level by exploiting historical and evolutionary recombination events at the population level (Zhu *et al.*, 2008).

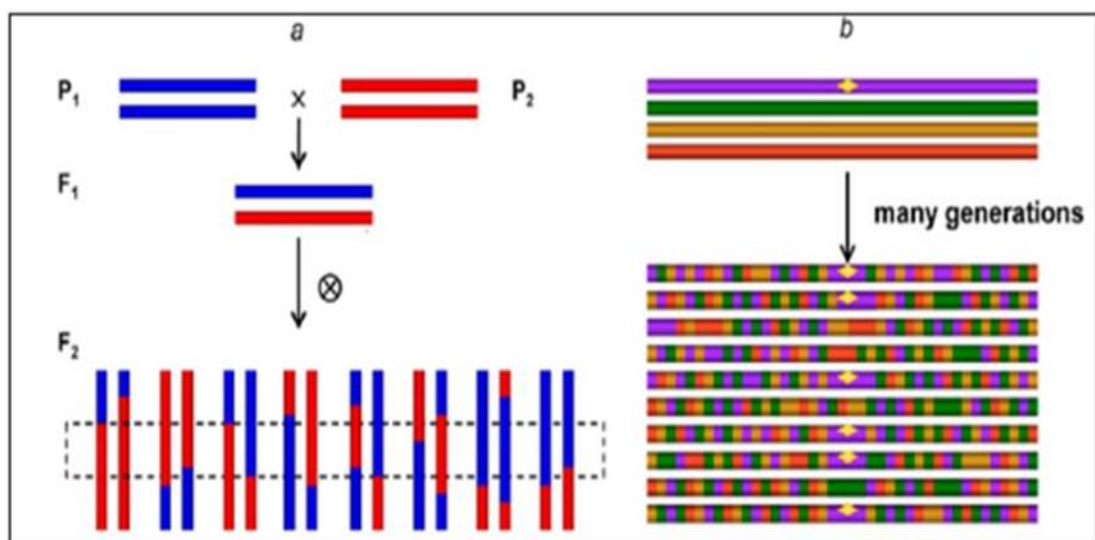


Figure 2. Schematic comparison of linkage mapping with designed mapping populations (a) and association mapping with diverse collections (b) (Zhu *et al.*, 2008).

From the above diagram (**Figure 2**): panel “a” indicates linkage analysis using F_2 design as an example and there are only few opportunities for recombination to occur within families and pedigrees of known ancestry, resulting in relatively low mapping resolution. In association mapping (i.e. panel “b” haplotype) historical recombination and natural genetic diversity were exploited for high resolution mapping. Linkage disequilibrium between a functional locus (yellow diamond for mutated allele) and molecular markers is low except for those within very short distance.

This method has been first applied in human genetics mainly because of the early adoption of large-scale genotyping strategies and the necessity of exploiting population based samples for studying complex human diseases (Stein and Elson, 2009) but its application in crop genetics and crop improvement has been becoming popular (Gupta *et al.*, 2005; Zhu *et al.*, 2008).

Association mapping measures the degree to which alleles at a marker locus are associated with the trait of interest at a population level. The degree to which this occurs depends on the strength of linkage disequilibrium between the marker and the locus that affects the trait. Association mapping not only allows mapping of genes/QTLs with higher level of confidence, but also allows detection of genes/QTLs, which will otherwise escape detection in linkage-based QTL studies based on the planned populations (Gupta *et al.*, 2005). In humans, association analysis has already proved extremely useful in tagging a large number of Mendelian genes, particularly those involved in various diseases (Botstein and Risch, 2003) but in recent times this method has been increasingly adopted to many plants with great success (Zhu *et al.*, 2008).

Association mapping has continued to gain favorability in genetic research because of advances in high throughput genomic technologies, interests in identifying novel and superior alleles, and improvements in statistical methods and bioinformatics. It involves searching for genotype-phenotype correlations among unrelated individuals and has the potential to identify a single polymorphism within a gene that is responsible for phenotypic differences. Its high resolution is accounted for by the historical recombination accumulated in natural populations and collections of landraces, breeding materials and varieties. By exploiting broader genetic diversity, association mapping offers three main advantages over linkage mapping; mapping resolution, allele number and time saving in establishing a marker-trait association and its application in a breeding program (Flint-Garcia *et al.*, 2003; Yu and Buckler, 2006). Although association mapping presents clear advantages over linkage mapping, they are often applied in conjunction, especially to validate the associations identified by association mapping, thus reducing spurious associations. Since most of the traits important for environmental fitness and agricultural value are quantitative in nature (Yu & Buckler, 2006), there is tremendous interest in using association mapping to examine them.

The general approach of association mapping in plants includes the following six basic steps: (1) Selection of a group of individuals from a natural population or germplasm collection with wide coverage of genetic diversity that may include landraces, elite varieties, wild relatives and exotic accessions; (2) A target phenotype (e.g. yield, quality, disease tolerance, drought tolerance, etc.) for the selected genotypes, preferably evaluated in different environments and multiple replication/trial design; (3) Genotypes are then scanned with suitable molecular

markers (AFLP, SSRs, SNPs); (4) Assessment of the population structure (the level of genetic differentiation among groups within a sampled population of individuals) and kinship (coefficient of relatedness between pairs of each individuals within a sample) are determined to avoid false positives; (5) Quantification of LD extent using different statistics like D , D' or r^2 and (6) Based on the information gained through quantification of LD and population structure, correlation of phenotypic and genotypic data with the application of an appropriate statistical software that reveals “marker tags” positioned within close proximity of targeted trait of interest.

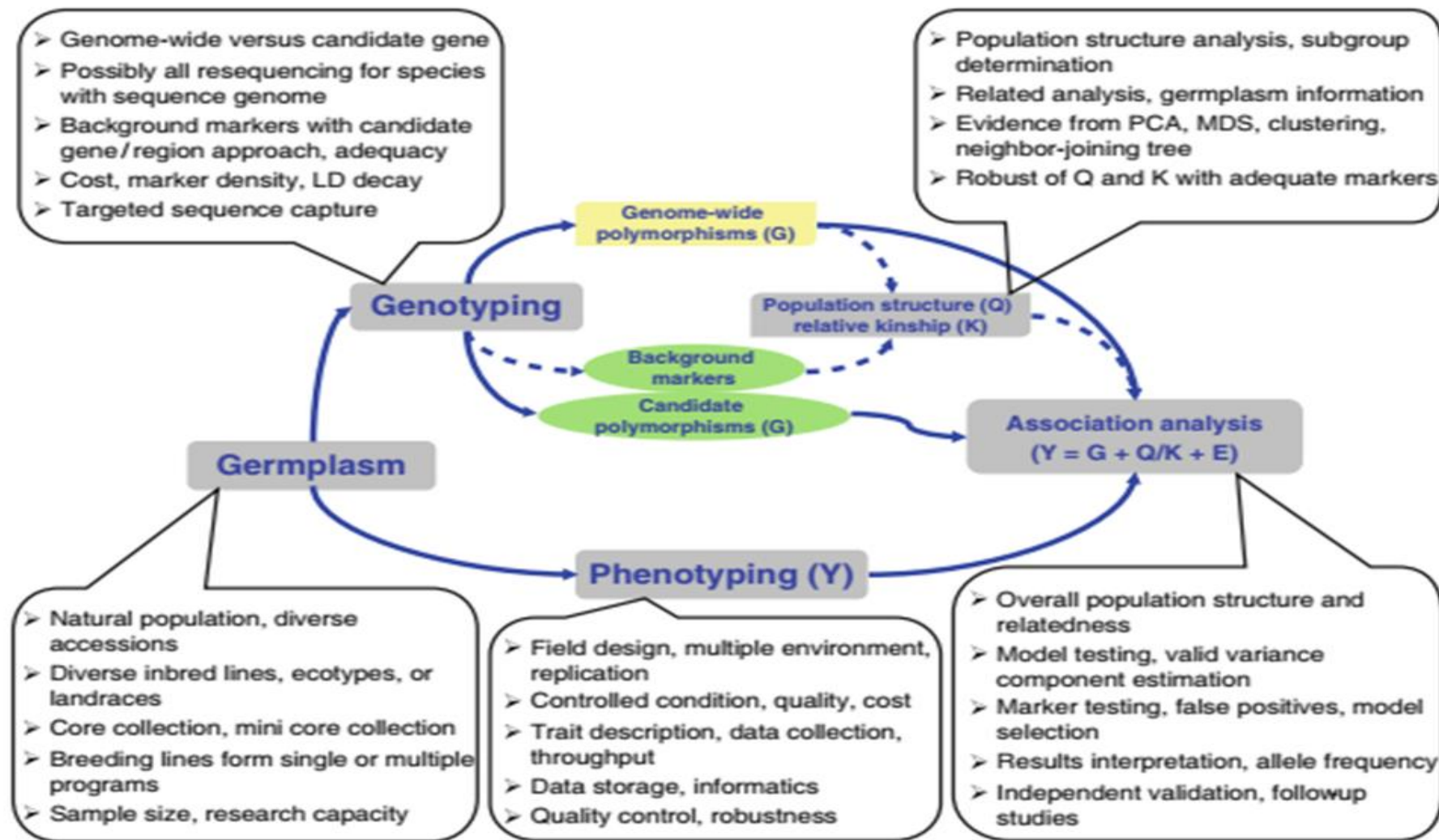


Figure 3. General procedures of association mapping and highlights of different steps (Yu *et al.*, 2013).

Association mapping broadly falls into two major classes: (1) Candidate-gene association mapping, which relates candidate gene polymorphisms with phenotypic variations of the traits (Yan *et al.*, 2010); and (2) Genome-wide association mapping (GWAS), which surveys genetic variation in the whole genome using a large number of markers to detect regions associated with the phenotype (Hirschhorn and Daly, 2005; Zhu *et al.*, 2008; Yu *et al.*, 2013). While candidate-gene association studies specifically target genes with known functions in the trait of interest (Tabor *et al.*, 2002), genome-wide association study scans the entire genome for detecting marker-trait associations with a large number of markers (Hirschhorn and Daly, 2005).

2.6. Genome-wide Association Study (GWAS)

Genome-wide association mapping (GWAS) is a strong statistical tool that includes genotyping a large collection of accessions with tens of thousands of SNPs through the whole genome and conduct association analysis with phenotypic trait(s) of interest. GWAS involves testing for association in most of the segments of the genome, by genotyping densely distributed genetic marker loci covering all chromosomes. The hypothesis under consideration is simple ‘one (or more) of the genetic loci being considered is either causal for the trait or in linkage disequilibrium with the causal locus’.

The GWAS era was born as biotechnology companies, including Affymetrix, Illumina and Perlegen, launched competing platforms to simultaneously genotype hundreds of thousands of SNPs. Genome-wide association study was initially developed to study the human genome (Wang *et al.*, 2005). It has been extensively conducted to dissect the causal genes of complex human diseases for the past one decade (Manolio *et al.*,

2009). The contribution of GWAS work to understanding of the genetic basis and molecular mechanisms of common disease is evident and over 2,000 human GWAS reports appeared in the scientific journals (Andreas and Christensen, 2016).

The most common type of variants is the single-nucleotide polymorphism (SNP) which describes changes to an individual DNA base. The different forms of the same gene containing variable SNPs within the same site(s) are typically called alleles. GWAS methods are chiefly concerned with determining alleles associated with various SNPs in each study subject, and making statistical comparisons to identify SNPs or genes associated with a particular trait. If a certain allele is more common among individuals with certain disease than healthy ones, which is interpreted as evidence that this allele or perhaps another nearby variant may cause the disease or at least increase the risk of the disease (Andreas and Christensen, 2016). Most SNPs result from a historical mutation event and due to this ancestry, each new allele is initially associated with the other alleles present on the particular chromosomal background where it arose. The specific set of alleles observed together on a single chromosome or part of a chromosome is called a haplotype. New haplotypes are formed by additional mutations or by chromosome recombination during meiotic cell division. Haplotypes tend to be conserved, especially among individuals with recent shared ancestry and haplotype conservation is a very important factor for GWAS (Hayes, 2013). The genetic variant that causes a particular trait may not be directly tested in the GWAS, but its signature may still be evident through the association of SNPs occurring within the same haplotype. GWAS utilizes the linkage disequilibrium (LD), which is the non-random association of alleles or haplotypes at two or more

loci, to infer the inherent associations between phenotypic variations and marker polymorphisms (Mackay and Powell, 2007).

2.6.1. Design of GWAS Analysis

GWAS is designed to assess the genetic determinants of almost any kind of phenotypic trait. While conducting GWAS is quite straightforward, key to finding an answer to a biologically relevant query is important. Hence, critical experimental design and analysis is required. A poorly designed GWAS will not identify any genome region at all, or, even worse, might identify genome regions that are not relevant for the biological question. Several issues should be critically considered in GWAS study design, including selection of a genotyping platform, population/sample size and collection (phenotyping), linkage disequilibrium, population structure, statistical analysis methods and their power and correction for multiple testing.

2.6.1.1. Genotyping platforms

Microarray/DNA chip technology, that allows the detection of large number of SNP polymorphisms within a population, has been widely used to genotype in GWAS studies. Once a comprehensive SNP data set is available for a species, a well-designed microarray can be produced and generally, the technology is then cost efficient and the process is relatively convenient. Microarrays involve three basic principles: 1) the array contains immobilized allele-specific oligonucleotide probes, which are short pieces of synthesized DNA complementary to the sequence of the target DNA; 2) fragmented nucleic acid sequences of the target, labeled with fluorescent dyes; and 3) a detection system that records and interprets hybridization signals measuring essentially genetic similarity. DNA chips are designed to test as many SNPs as

practically possible and currently up to about five million human SNPs included and nearly all GWAS in human genetics have used microarray technology (Andreas and Christensen, 2016). Microarray based genotyping has been applied in crops such as rice (McNally *et al.*, 2009; Zhao *et al.*, 2011), wheat (Wang *et al.*, 2014; Maccaferri *et al.*, 2016; Liu *et al.*, 2017) and maize (Ganal *et al.*, 2011; Li *et al.*, 2013).

High-throughput sequencing-based genotyping method is the other platform (Schneeberger and Weigel, 2011). For genotyping of recombinant populations, a method that utilizes low-coverage whole-genome re-sequencing data was developed (Huang *et al.*, 2009; Zhao *et al.*, 2010). The low-coverage whole-genome re-sequencing approach was also used in the genotyping of natural populations through completely different computation methods (Huang *et al.*, 2010). Some crops such as maize, barley, and wheat have huge genomes, and whole-genome resequencing for these crops could be still expensive. However, there are now several alternatives to sequence the whole genome for such crops. One method is to generate restriction-site-associated DNA tags (e.g., using *SbfI* or *EcoRI*) and sequence them to identify polymorphic markers (Baird *et al.*, 2008). A similar approach is to cut the genomic DNA and ligate the genomic fragments to bar-code adapters to prepare a multiplex sequencing library (Elshire *et al.*, 2011). Genotyping by sequencing (GBS) has been used in maize, sorghum, and barley and these applications showed that this method is efficient for large-scale, low-cost genotyping despite the limitations in SNP number and distribution (Elshire *et al.*, 2011; Morris *et al.*, 2012; Roday *et al.*, 2013).

Another approach, known as RNA sequencing (RNA-seq) based genotyping, is to retrieve genotype from RNA-seq data. Despite the existence of abundant variation in

genome size for different crops, there are no significant variations in number of genes or total gene sizes. Since most repetitive regions are ignored, undertaking transcriptome sequencing for SNP calling rather than whole-genome resequencing is quite cost effective. For example, a recent study genotyped a large number of SNPs from 368 maize transcriptomes and then used the RNA-seq data for expression profile analysis and expression QTL (eQTL) mapping simultaneously (Li *et al.*, 2013). However, RNA-seq-based sequencing has several limitations. Since the SNP density in genic regions is much lower than that in intergenic regions, the number of SNPs called from RNA-seq data may not be large enough for GWAS, especially for high-LD crops. The existence of a strong bias in SNP distribution raises another problem: In a particular tissue at a particular time point, many genes have very low or even no expression and thus cannot be used in genotyping, but RNA preparation of multiple tissues at multiple time points for a large population would greatly increase the workload. Exon-sequencing-based genotyping, facilitated by exon capture, can also be applied to the mapping of some large, complex crop genomes (Mascher *et al.*, 2013; Ng *et al.*, 2009; Wang *et al.*, 2010).

2.6.1.2. Phenotyping

Application of next-generation sequencing technology has had a major impact on the genomics of different crops in a short period. However, phenomics, a new discipline involving the characterization of the full set of phenotypes of a given species, still lags far behind genomics. In previous decades, the key questions of genomics involved why and how to sequence genomes. However, now, the new challenge we have been facing is phenomics (Houle *et al.*, 2010). Phenotyping is one of the most determining parts for GWAS analysis. GWAS will have a strong power to identify the

causative gene when the phenotypic variation is the result of genetic rather than environmental variation (i.e., high heritability). Trait heritability depends on the quality of the phenotypic data; the more precisely phenotyping is done, the higher the heritability and the more power to detect causal variants through GWAS (Burghardt *et al.*, 2017). The second reason for thinking carefully about phenotyping is because the probability of GWAS succeeding is directly related to the number and effect sizes of genes responsible for variation: the fewer the genes and the larger the effects, the more power for identifying the genes. Given the diverse nature of an association mapping panel in crops, it is critical to consider the influence of some other traits on the target trait. For example, flowering time commonly affects the expression of other correlated traits. It might be worthwhile to block a field by flowering time if traits of interest are dependent on developmental transitions. Other issues that need be considered in phenotyping include photoperiod sensitivity, lodging, and susceptibility to prevalent pathogens because these traits affect the measurement of other morphological or agronomic traits at field condition (Zhu *et al.* 2008).

Traditional phenotyping tools, which inefficiently measure a limited set of phenotypes, have become a bottleneck in functional genomics and plant breeding studies (Furbank and Tester, 2011). In GWAS, traditional phenotyping is yet important but it is inefficient and highly laborious, and progress in phenotyping technologies is required to accelerate genetic mapping and gene discovery (Han and Huang, 2013; Hwang *et al.*, 2014). Since GWAS often involves a relatively large number of diverse accessions, phenotypic data collection with adequate replications across multiple years and multiple locations is challenging (Zhu *et al.* 2008). However, multidisciplinary techniques, including novel imaging sensors, image

analysis, spectroscopy, robotics and high-throughput computing, has enabled the development of high-throughput and large-scale non-invasive phenotyping infrastructures (Spalding and Miller, 2013; Yang *et al.*, 2013).

2.6.1.3. Linkage Disequilibrium

Linkage disequilibrium (LD), also known as gametic phase disequilibrium, gametic disequilibrium, and allelic association refers to a non-random association between alleles at different loci (Flint-Garcia *et al.*, 2003; Gupta *et al.*, 2005; Mackay and Powell, 2007). Understanding the LD pattern in germplasm is important for selecting the marker density required for GWAS, experimental design needed to perform an association analysis, and for defining identified QTL regions (Siol *et al.*, 2017). It is a pair-wise measurement between polymorphic sites. If one locus has alleles A and a with frequencies P_A and $1 - P_A$, and a second has alleles B and b with frequencies P_B and $1 - P_B$, then at equilibrium, even though the loci are linked, the expected haplotype frequencies are the product of the constituent allele frequencies. For example, using the AB haplotype:

$$P_{AB} = P_A \times P_B$$

Any departure from this state of linkage equilibrium is called linkage disequilibrium and can be estimated as:

$$D = P_{AB} - P_A \times P_B$$

Where P_{AB} is the observed value; P_A and P_B are the expected frequencies; D is the coefficient of linkage disequilibrium. At equilibrium, $D = 0$. In absence of other forces, recombination through random mating breaks down the LD with $D_t = D_0 (1 - r)^t$, where D_t is the remaining LD between two loci after t generations of random mating from the original D_0 ; r is the recombination fraction between the two loci.

Coefficient of linkage disequilibrium (D) can be difficult to interpret and its range depends on the allele frequency, and it is not symmetrical about zero. It is therefore usually rescaled to give it a range from 0 to 1. Several statistics have been proposed for LD including D' , r^2 , R , D^2 , D^* , Q^* , F' , X (2), and δ . All statistics measure the difference between the observed and expected haplotype frequencies (Flint-Garcia *et al.*, 2003; Gupta *et al.*, 2005). Both D' (Lewontin, 1964) and r^2 (Hill and Robertson, 1968) have been widely used to quantify LD (Gupta *et al.*, 2005). For two bi-allelic loci, D' and r^2 have the following formula:

$$D' = \frac{|D|}{D_{max}}$$

Where $D_{max} = \min(p_A p_B, p_a p_b)$ if $D < 0$; $D_{max} = \min(p_A p_b, p_a p_B)$ if $D > 0$;

The D' is the standardized disequilibrium coefficient, which mainly measures recombinational history and is therefore useful to assess the probability of historical recombination in a given population.

The r^2 can be defined as the squared value of the Pearson's correlation coefficient (product moment) of allelic frequencies at two loci and calculated as:

$$r^2 = \frac{D^2}{p_A p_a p_B p_b}$$

Both parameters vary in the interval from 0 to the value of 1. While D' measures only recombination differences, r^2 summarizes both recombination and mutation history. r^2 is also an indicative of how markers might be correlated with QTL of interest, so that for GWAS, r^2 is often preferred (Abdallah *et al.*, 2003).

Although the performance of both statistics are affected by small sample size and low allele frequencies, r^2 is less sensitive to sample size and better in indicating how markers might be correlated with QTL of interest (Flint-Garcia *et al.*, 2003). The value of r^2 approaches one when the frequency of co-segregation of alleles at two loci is high while an r^2 value of zero shows the co-occurrence of alleles at two loci does not differ from what would be expected under random sampling (Ersoz *et al.*, 2009).

Linkage disequilibrium increases due to selection in a population, small population size, inbreeding, genetic isolation between lineages, population subdivision, low recombination rate, population admixture, genetic drift and epistasis. While factors like outcrossing, high recombination rate, high mutation rate, gene conversion, high population size etc., lead to a decrease/disruption in LD (Gupta *et al.*, 2005).

To summarize the structure and patterns of LD, r^2 for pairwise combinations of alleles are plotted against the genetic distances among alleles on a chromosome. This type of graphical display is known as a LD decay plot, which allows fitting decay curve to estimate LD decay for a chromosome or for an entire genome (Flint-Garcia *et al.* 2003; Gupta *et al.*, 2005; Abdurakhmonov and Abdukarimov, 2008). Broadly, the extent of LD decay over genetic distance occurs at a slower rate in self-pollinated crops such as *Arabidopsis*, rice, wheat, barley and sorghum than cross-pollinated crops such as maize as the number of effective recombinations is lower in self-pollinated crops compared to cross-pollinated crops. Studies on rates of LD decay in various plants reveal tremendous variation in the extent of linkage disequilibrium including *Arabidopsis thaliana* (Nordborg *et al.*, 2002; Nordborg *et al.*, 2005), maize (Ching *et al.*, 2002; Palaisa *et al.*, 2003), barley (Caldwell *et al.*, 2004; 2006),

sorghum (Hamblin *et al.*, 2005), bread wheat (Gurung *et al.*, 2014) and durum wheat (Maccaferri *et al.*, 2005; Liu *et al.*, 2017).

2.6.1.4. Population Structure

The GWAS approach has been seen with skepticism by plant genetics and breeding communities until recently because of false positive/spurious associations as a consequence of the confounding effect from population structure. Population structure often leads to a genome-wide LD between unlinked loci (Sneller *et al.*, 2009). Because of non-random mating, isolation or artificial selection, structured populations exist more or less in any plant population. Consequently, genetic loci could be spuriously associated with a trait when there is no real association. The probability of a false positive/Type I error increases in association mapping studies if the population structure is not appropriately accounted for (Flint-Garcia *et al.*, 2003; Gupta *et al.*, 2005; Maccaferri *et al.*, 2005, 2011; Yu *et al.*, 2006; Letta *et al.*, 2013). False positives are easy to control, but only at the expense of true positive discovery or statistical power. For example, a stringent association test threshold is an effective way to control the false positive rate, but the numbers of true positives are reduced at the same time. A desirable solution is to reduce false positives without compromising statistical power. This solution is critical because the inheritance of most agriculturally important traits is controlled by many genes, which individually have small effects or rare alleles (Buckler *et al.*, 2009). Several statistical methods have been developed to account population structure during association studies thereby increasing the application of GWAS in QTL detection in plants. Both distance and model-based estimations of population structure have been used (Maccaferri *et al.*, 2005; Yu *et al.*, 2006; Camus-Kulandaivelu *et al.*, 2007; Peleg *et al.*, 2008).

Distance-based estimates of population structure are generally based on clustering of individuals based on pair-wise genetic distance estimates between individuals (Nei, 1972, 1978; Rogers, 1972). These methods are visually tempting but are not suitable for statistical inference (Pritchard *et al.*, 2000). In contrast, model-based methods, appropriate and commonly used methods, assign individuals probabilistically to one or more subpopulations (Pritchard *et al.*, 2000).

A unified mixed-model, which was proposed by Yu *et al.* (2006) has been widely used in GWAS studies of various plants. This method determines relatedness of samples in populations, resulting in a reduction in both Type I and Type II errors, by combining population structure (Q) with relative kinship (K), accounting for multiple levels of relatedness. This model accommodates both fixed and random effects.

The Q+K mixed model is represented with the following equation:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{S}\boldsymbol{\alpha} + \mathbf{Q}\mathbf{v} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of phenotypic observations; $\boldsymbol{\beta}$ is a vector of fixed effects other than marker or population structure; $\boldsymbol{\alpha}$ is a vector of marker effects; $\mathbf{u}$ is a vector of random polygenic background effects; $\mathbf{e}$ is a vector of residuals; $\mathbf{Q}$ is a matrix from structure relating $\mathbf{v}$ to $\mathbf{y}$; and $\mathbf{X}$, $\mathbf{S}$ and $\mathbf{Z}$ are incidence matrices of 1s and 0s relating $\mathbf{y}$ to $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$ and $\mathbf{u}$, respectively. The variances of the random effects are assumed to be $\text{Var}(\mathbf{u}) = 2\mathbf{K}\mathbf{V}_g$, and $\text{Var}(\mathbf{e}) = \mathbf{R}\mathbf{V}_R$, where $\mathbf{K}$ is an $n \times n$ matrix of relative kinship coefficients that define the degree of genetic covariance between a pair of individuals; $\mathbf{R}$ is an $n \times n$ matrix with the off-diagonal elements being zero and the diagonal elements being the reciprocal of the number of observations for which each

phenotypic data point was obtained; V_g is the genetic variance; and V_R is the residual variance. Best Linear Unbiased Estimates (BLUEs) of β , α , v (fixed effects), and Best Linear Unbiased Predictions (BLUPs) of u (random effect) are obtained by solving mixed model equations (Yu *et al.*, 2006). A publically available software STRUCTURE (Pritchard *et al.*, 2000) was developed to account for population structure and has been implemented in a number of crop species.

2.6.2. GWAS Statistical Analysis Approaches

Statistical procedures and analysis power are among the most critical areas in GWAS. The analysis methods for GWAS rely mostly on statistical inference to estimate associations between traits and genetic variants. Generally, a GWAS infers these associations through a hypothesis test with appropriate test statistics. For a qualitative trait, the frequency of the different phenotype values is often used to infer associations. Generally, the trait is classified into two sample sets (test and control) and the genotype frequency at each SNP locus in each set is calculated and used to form a contingency table. This table can then be used to calculate the odds ratio or relative risk that is used in the hypothesis test.

For a quantitative trait, a regression model is often used for an association study in which each SNP is an explanatory (or independent) variable and the phenotypic trait is the response (or dependent) variable. Different models for GWAS have been used and these models basically consider confounding effects in the materials and complex genetic interactions. Selecting optimal models enables accurate evaluation of associations between marker loci and numerous phenotypic traits.

2.6.2.1. GWAS Test using Single Marker Regression

From the numerous statistical methods employed in GWAS analysis, GWA test using single marker regression is the simplest one (Hayes, 2013).

In a random mating population with no population structure, the association between a marker and a trait can be tested with single marker regression as:

$$\mathbf{y} = \mathbf{W}\mathbf{b} + \mathbf{X}\mathbf{g} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of phenotypes, $\mathbf{W}$ is a design matrix assigning records to phenotypes fixed effects, $\mathbf{b}$ is a vector of fixed effects (e.g., the mean, population structure effects, and age), $\mathbf{X}$ is a design matrix allocating records to the marker effect, $\mathbf{g}$ is the effect of the marker, and $\mathbf{e}$ is a vector of random deviates $\mathbf{e}_{ij} \sim N(0; \sigma_e^2)$, where σ_e^2 is the error variance (Hayes, 2013). The underlying assumption here is that the marker will only affect the trait if it is in linkage disequilibrium with an unobserved QTL. The null hypothesis is that the marker has no effect on the trait, while the alternative hypothesis is that the marker does affect the trait (because it is in LD with a QTL).

There are different determining factors for the power of association test to detect a QTL by testing the marker effect and these are: I) The r^2 between the marker and QTL; II) The proportion of total phenotypic variance explained by the QTL; III) The number of phenotypic records; IV) The allele frequency of the rare allele of the SNP which determines the minimum number of records used to estimate an allele effect and V) The significance level set by the experimenter. The power is the probability that the experiment will correctly reject the null hypothesis when a QTL of a given size of effect really does exist in the population.

2.6.2.2. GWAS Test using Haplotypes

A haplotype is a set of DNA variations, or polymorphisms/SNPs, that tend to be inherited together. Instead of using a single marker, haplotypes of markers could be used in the genome-wide association studies. The effect of haplotypes across the genome would then be tested for their association with phenotypes. The justification for using haplotypes is that marker haplotypes may be in greater linkage disequilibrium with the QTL alleles than single markers. If this is true, then the r^2 between the QTL and the haplotypes is increased, thereby increasing the power of the experiment (Hayes, 2013). Most of the time, two haplotypes are identical because they are derived from the same common ancestor (i.e they are identical by descent IBD). If the haplotypes are IBD, then the chromosome segments will also carry the same QTL alleles. As the probability of two identical haplotypes being IBD increases, the proportion of QTL variance explained by the haplotypes will increase, as marker haplotypes are more and more likely to be associated with unique QTL alleles. This is particularly true for QTL with rare (low frequency) minor alleles (Hayes, 2013).

Several studies have proven the advantages of haplotype analysis over single marker analysis in QTL identification (Pryce *et al.*, 2010). However, there are some features which potentially limit their value over single markers, including: 1) It requires sorting of genotypes into haplotypes and this may not be a trivial work; 2) The number of effects which must be estimated increases (i.e. for a single marker there is one effect to estimate if an additive model is assumed, while for marker haplotypes there are potentially a large number of effects to estimate depending on the number of markers in the haplotype and 3) Some simulation results which show benefits of

marker haplotypes rely on increasing the density of markers in a given chromosome segment to achieve this but this may not be possible in practice (Pryce *et al.*, 2010).

2.6.2.3. GWAS using an Identical by Descent (IBD) Approach

The IBD is quite different from both single marker or haplotypes block regression techniques, as now the effect of a putative QTL is explicitly modeled, rather than assuming the marker is associated with the QTL (Hayes, 2013).

$$Y_i = \mu + \mu_i + \mathbf{v}\mathbf{p}_i + \mathbf{v}\mathbf{m}_i + e_i$$

where $\mathbf{v}\mathbf{p}_i$ and $\mathbf{v}\mathbf{m}_i$ are the effects of the QTL alleles carried on the i^{th} individual's parental chromosomes, respectively. In this model, the assumption is that each individual carries two unique QTL alleles, and so there are two QTL effects fitted for each individual.

Marker haplotype information will be then used to infer the probability that two individuals carry the same QTL allele at a putative QTL position. The existence of LD implies there are small segments of chromosome in the current population, which are descended from the same common ancestor. These IBD chromosome segments will not only carry identical marker haplotypes; if there is a QTL somewhere within the chromosome segment; the IBD chromosome segments will also carry identical QTL alleles. Therefore, if two individuals carry chromosomes which are likely to be IBD at a point of the chromosome carrying a QTL, then their phenotypes will be correlated (Hayes, 2013).

2.6.2.4. GWAS by Fitting all SNPs Simultaneously

There are limitations raised in single SNPs or haplotype methods. The first one is related with multiple testing problems. Thousands of tests are run, so the significance level should be very stringent to take this into account and the setting of a significance threshold combined with the testing of so many marker effects. This means the markers most likely to exceed the threshold with those with favorable error terms, so that the significant markers have overestimated effects. The other problem is unable to define the specific region containing the true mutation as a large number of SNPs could be in LD with the QTL and this is particularly true for plants with high LD. Fitting all SNPs simultaneously could solve these problematic issues and this involves fitting the same models that have been proposed for genomic prediction (Hoggart *et al.*, 2008).

This can be achieved by fitting the SNPs as random effects (e.g., derived from a distribution), with different prior assumptions on the distribution of possible SNP effects (e.g., a Bayesian approach) (Meuwissen *et al.*, 2001). The Model is:

$$\mathbf{y} = \mathbf{1}_n'\boldsymbol{\mu} + \mathbf{X}\mathbf{g} + \mathbf{e}$$

where $\mathbf{g}$ is now a vector of SNP effects. The simplest assumption is that the SNPs effects are derived from a normal distribution, in a SNPBLUP or ridge regression (Meuwissen *et al.*, 2001).

2.6.3. Current Achievements of GWAS

The use of next-generation sequencing technologies in the context of GWAS makes it possible to genotype larger populations of plants with a higher density of markers than was previously possible, and this contributes directly to increased mapping

resolution. Many features related to plant growth and developments have been approached through GWAS successfully. The landmark study of plant GWAS encompassed 107 traits of *Arabidopsis thaliana* and many of them were related to development and flowering time (Atwell *et al.*, 2010). Soon after, many GWAS approaches have identified previously known as well as novel loci underlying variation of flowering time in *A. thaliana* (Brachi *et al.*, 2010, 2013; Li *et al.*, 2010, 2014).

In maize (*Zea mays*), a joint linkage analysis and GWAS using Nested Association Mapping (NAM) population (NAM-GWAS) (Hung *et al.*, 2012) and subsequent GWAS using a larger number of SNPs indicated that *ZmCCT*, a homologue of the *Arabidopsis* flowering gene *CONSTANS* (Puterill *et al.*, 1995), underlies variation in flowering time, ear height and plant height through a polymorphism in a CACTA-like transposable element inserted in the promoter of *ZmCCT*. In similar ways, GWAS for flowering time variation of several crop plants have been successfully studied including maize (Hao *et al.*, 2011; Boucht *et al.*, 2013; Roday *et al.*, 2013; Van Inghelandt *et al.*, 2013; Xue *et al.*, 2013), rice (*Oryza sativa*) (Zhao *et al.*, 2011; Huang *et al.*, 2012), wheat (*Triticum aestivum*) (Zanke *et al.*, 2014), barley (*Hordeum vulgare*) (Lorenz *et al.*, 2010; Cockram *et al.*, 2012; Pasam *et al.*, 2012; Munoz-Amatriain *et al.*, 2014) common bean (*Phaseolus vulgaris*) (Galeano *et al.*, 2012), pearl millet (*Pennisetum glaucum*) (Saidou *et al.*, 2014).

Like flowering time, other highly relevant plant traits have been a target with GWAS approach. Seed-related traits are of high relevance for breeding in crops, as well as for fitness and adaptation in wild species. In rapeseed (*Brassica napus*), loci associated

with seed quality and seed weight-related traits were identified with GWAS using a collection of inbred lines originating from geographically diverse regions (Li *et al.*, 2014). Causal genes for variation in metabolites in *A. thaliana* seeds could be identified (Angelovici *et al.*, 2013). GWAS for seed-related traits have also been reported and could be able to discover novel candidate genes for maize (Hao *et al.*, 2011; Xue *et al.*, 2013; Huang *et al.*, 2013), rice (Zhao *et al.*, 2011; Huang *et al.*, 2012; Chen *et al.*, 2014; Yang *et al.*, 2014), barley (Cockram *et al.*, 2010; Pasam *et al.*, 2012; Munoz-Amatriain *et al.*, 2014; Cuesta-Marcos *et al.*, 2010), oat (*Avena sativa*) (Newell *et al.*, 2012), soybean (*Glycine max*) (Hwang *et al.*, 2014), cowpea (*Vigna unguiculata*) (Lucas *et al.*, 2013; Muchero *et al.*, 2013), common bean (Galeano *et al.*, 2012), tomato (*Solanum lycopersicum*) (Shirasawa *et al.*, 2013; Sauvage *et al.*, 2014).

GWAS have used *A. thaliana* root as a powerful model for dissecting molecular processes that underlie the quantitative regulation of organ growth and development. A high throughput root phenotyping pipeline played a key role in this case. It enables ease of phenotyping with large numbers of young plants, large-scale image acquisition and automated trait quantification from these images. Using automated image analysis on a large set of root images, 35 candidate genes could be identified for a diverse set of traits related to primary root growth. The most significant SNP in this study could be linked with a *CALCIUM SENSOR RECEPTOR* gene which regulates the elongation rate of the primary root (Slovak *et al.*, 2014). An investigation of root growth responses under different nitrogen conditions identified two genes underlying lateral root length under low and high nitrogen conditions (Gifford *et al.*, 2013). GWAS identified root allometry (i.e., the relative shape of the root system) significantly varied in response to different combinations of alleles and

growth conditions and *ROOT SYSTEM ARCHITECTURE 1*, a putative tyrosine transaminase gene, and *PHOSPHATE 1* have been identified as corresponding genes to this allometry trait variation (Rosas *et al.*, 2013). In rice, the identification of major QTLs for root depth has been instrumental in increasing adaptation to low water availability (Steele *et al.*, 2013) as well as for the positional cloning of *deeper rooting 1 (DRO1)* (Uga *et al.*, 2013). GWAS could identify Major QTL clusters controlling different root system architectural (RSA) traits in durum wheat (*Triticum turgidum* var. *durum*) (Maccaferri *et al.*, 2016).

Genome-wide association mapping successfully implemented to identify causal genes in different plants for yield and related traits (Zhao *et al.*, 2011; Sukumaran *et al.*, 2015; Mengistu *et al.*, 2016), stress resistance/tolerance i.e biotic (Nemri *et al.*, 2010; Kump *et al.*, 2011; Zila *et al.*, 2013) and abiotic (Hao *et al.*, 2011; Long *et al.*, 2013; Famoso *et al.*, 2011), and quality-related traits (Huang *et al.*, 2012; Li *et al.*, 2012; Newell *et al.*, 2012; Morris *et al.*, 2013; Shu and Rasmussen, 2014).

2.6.4. Limitations of GWAS

Nonetheless, GWAS have proven to be effective at detecting genes/QTLs contributing to phenotypic variation in numerous plant species, the method has its own limitations. Identifying some genes that contribute to variation is far from identifying the complete genomic basis of variation, and unless conducted with tens of thousands of accessions with thousands or millions of SNPs, GWAS is unlikely to identify genes of truly small effect (Bush and Moore, 2012). Second, since heterozygotes will have the same phenotype as that of the homozygous dominant, recessive alleles are usually not identified through this approach. Epistatic interactions,

population stratification and identifying genes responsible for phenotypic plasticity (G x E) makes GWAS a more complicated approach and unless accounted and controlled appropriately, they will lead to a false-positive result (Burghardt *et al.*, 2017).

2.7. Genomic Dissection for Drought Adaptive Traits in Wheat

Among all abiotic stresses most affected by climate change, drought is the major one curtailing global wheat production (Tuberosa and Maccaferri, 2015). Drought is one of the most common environmental stresses that affects growth and development of plants through alterations in metabolism and gene expression (Leopold, 1990). It continues to be a challenge to agricultural scientists in general and to plant breeders in particular, despite many decades of research. It is a permanent constraint to agricultural production in many developing countries and occasionally in developed ones (Ceccarelli and Grando, 1996).

Adapting crops to water-limited environments and improving their efficiency for water use, which have been always major objectives of plant breeding, will be key elements for developing climate-resilient varieties that are capable of producing “more food per drop” (Ortiz *et al.*, 2007). Drought tolerance is a quantitative trait, with complex phenotype and genetic control (McWilliam, 1989). Although conventional breeding has steadily increased crop productivity under drought conditions and across a broad range of environmental constraints, the present rate of increase in wheat productivity is insufficient to meet food security globally (Tuberosa and Maccaferri, 2015). Genomics-assisted crop improvement provides novel opportunities to enhance the yearly rate of increase in wheat yield while advancing our understanding of the genetic and functional basis of the adaptive response to

water-limited conditions (Habash *et al.*, 2009; Fleury *et al.*, 2010; Able and Atienza, 2014 ; Tuberosa and Pozniak, 2014; Tuberosa *et al.*, 2014).

Given the complexity of the genetic control of drought tolerance (multigenic, low-heritability, and high GxE interactions), marker-assisted selection has not contributed significantly to variety improvement for dry environments and breeding has relied on direct phenotypic selection. There are additional problems in investigating the genomics of drought tolerance in species like wheat, hence most pathways and candidates are effectively studied in model species with smaller and sequenced genomes such as *Arabidopsis* and even amongst the cereals there are more extensive data available for rice and maize when compared with wheat. However, recent technological advances and the imperative to ensure sustainable food production has driven research programs to improve this crop genetically despite the size and complexity of the genome (Fleury *et al.*, 2010). Breeding for drought tolerance is further complicated by the fact that several types of abiotic stresses can challenge crop plants simultaneously. In addition, screening conditions adopted under controlled conditions usually provide a rather poor surrogate of the dynamics of the drought episodes that crops are exposed to in the field (Passioura, 2010; Tuberosa, 2012).

Drought tolerance comprises three different mechanisms: 1) dehydration avoidance 2) drought escape and 3) dehydration tolerance mechanisms (Blum, 1988). Drought escape through early flowering and/or short growth duration is advantageous in environments with terminal drought stress and where physical or chemical barriers inhibited root growth (Blum, 1988; Blum *et al.*, 1989). Dehydration avoidance can be defined as the plant's ability to retain a relatively higher level of hydration under

conditions of soil or atmospheric water stress. Root characteristics are important traits which increase the plant's water uptake ability under atmospheric water stress conditions (Blum, 1988).

In previous times, efforts have focused on shoot characteristics rather than on roots, owing in part to the challenges of *in situ* examination of roots and the complex influence of the environment on their growth (Tuberosa *et al.*, 2002b). Roots play several essential roles in the plant life cycle, including anchoring to the soil, mechanical support to stems, uptake of water and nutrients (Osmont *et al.*, 2007; Smith and De Smet, 2012) and, more in general, governing the adaptive response of the plant to unfavorable soil conditions (De Dorlodot *et al.*, 2007; Reynolds and Tuberosa, 2008). The development of a deep and extensive root system is a drought-adaptive strategy that allows the plant to efficiently acquire water and nutrients from deep in the soil profile and helps the plant to meet evapotranspiration demands. Root growth and distribution play an important role in plant response to water availability, are central in determining the growth and yield of crops in water-limited environments, and are determined by both plant genotype and the soil environment (Hund *et al.*, 2008). The root system architecture describes the shape and structure of the root system, both of which have great functional importance. The shape defines the distribution of the roots in space and the way the root system occupies the soil. The root shape can be described through several geometrical criteria, as the lateral root extension or the root depth, or in more detail, as the distribution of the root length density in the soil. The root structure refers to the diversity of their components (root segments) and their relationships.

In view of this and the continuous improvement in high-throughput phenotyping, root system architecture (RSA) has been receiving increasing attention in terms of genetic dissection and the influence of root system architecture on yield and other agronomic traits has been widely reported for all major crops (Tuberosa *et al.*, 2002a, b; Gregory *et al.*, 2009; Habash *et al.*, 2009; Trachsel *et al.*, 2011; Cané *et al.*, 2014; Lobet *et al.*, 2014; Naz *et al.*, 2014; Petrarulo *et al.*, 2015; Maccaferri *et al.*, 2016).

2.8. Genetic Detection for Quality-related Traits in Wheat

Wheat grain characteristics generally include grain weight, shape, color, hardness, and other related traits. Grain size, which represents thousand grain weight, grain area and test weight and grain shape representing grain length, width and grain length width ratio, are a major component of wheat yield (Breseghello and Sorrells, 2006). Large grain size has been an important trait and it is usually represented in plant breeding practice by thousand grain weight, mainly determined by grain width, grain length and grain thickness (Su *et al.*, 2011). Grain size and shape also influences the milling and baking quality of wheat and geometrical models indicated that changes in grain shape and size could result in increases in flour yield of up to 5% (Röder *et al.*, 2008; Rasheed *et al.*, 2014). Wheat grain size and shape are a quantitative traits controlled by QTLs and several of these QTLs have been reported in previous studies (Campbell *et al.*, 2003; Dholakia *et al.*, 2003; Huang *et al.*, 2012; Röder *et al.*, 2008; Su *et al.*, 2011).

Ethiopian durum wheat has comprised a variety of grain colors that could be associated with the cultural use value of different kernel color types for various traditional purposes, which could ensure the conservation of the different

morphotypes by small-scale farming communities (Mengistu *et al.*, 2015). The collection encompasses white, yellow, amber, gray, brown, brown-purple and purple kernel colors (Eticha *et al.*, 2005; Mengistu *et al.*, 2015). Durum wheat landraces with purple kernel is endemic to Ethiopia (Zeven, 1991) and classified as *T. turgidum* ssp. *aethiopicum* (Eticha *et al.*, 2005).

Color of the kernel comes from the pigment it contains and two natural pigments (i.e. carotenoid and anthocyanin) exist in wheat grain. Carotenoids are responsible for many of the red, orange and yellow colors in nature (Humphries *et al.*, 2004). The yellowish-amber color of durum semolina comes from the carotenoid pigment found in the grain and has been used as one of the good quality indicators of semolina (CIE, 1986). Anthocyanins on the other hand accumulate in the pericarp or aleurone of durum wheat and provide the blue, purple and red colors of the grain (Ficco *et al.*, 2014). Both carotenoids and anthocyanins have an enormous importance in human health and nutrition (Humphries *et al.*, 2004).

Previous findings proved that wheat grain color is highly controlled by several genes/QTLs involved in pigment accumulation and proteins with regulatory role (Ficco *et al.*, 2014). Genes and QTLs for whole grain or flour color of both bread and durum wheat have been identified (Elouafi *et al.*, 2001; Mares and Campbell 2001; Groos *et al.*, 2002; Pozniak *et al.*, 2007; Sherman *et al.*, 2008; Blanco *et al.*, 2011; Li *et al.*, 2011; Tsilo *et al.*, 2011; Roncallo *et al.*, 2012; Crawford and Francki, 2013; Colasuonno *et al.*, 2014; Zhai *et al.*, 2016).

3. MATERIALS AND METHODS

The study is consisting of three main parts including: I) Genetic diversity, linkage disequilibrium and population structure; II) Genome-wide association analysis for seminal root system architecture traits; and III) Genome-wide association mapping for grain shape and color related traits

In this section, the materials and methods are sequentially marked for each of the explained parts followed by the results and discussion parts.

3.1. Genetic Diversity, Linkage Disequilibrium and Population Structure

3.1.1. Plant Materials

One hundred sixty seven Ethiopian durum landrace accessions collected from major wheat growing areas of the country and twenty five durum varieties released and cultivated in Ethiopia were assembled for the present genetic diversity analysis. Varieties were released by Debre Zeit Agricultural Research Center (DZARC) and Sinana Agricultural Research Center (SARC), Ethiopia in different years (1994 - 2010) and are under cultivation. All the landrace accessions and varieties used in this study are maintained by these two agricultural research centers as a single seed descent (SSD) progenies.

Landraces were originally collected from major wheat-producing areas of Ethiopia (**Figure 4**) including Bale, Gondar, Gojjam, Shewa, Tigray, Wollo, and twelve lines, which are originally from Ethiopia but currently cultivated in the USA. The detail of accessions is summarized in **Table 1**. Table 1 con't

Table 1. Description of Ethiopian durum wheat accessions used for the current study.

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release
EP001	WC-1no.4	Landrace	Wollo	DZARC	—
EP002	WC-1no.59	Landrace	Wollo	DZARC	—
EP003	WC-2no.85	Landrace	Wollo	DZARC	—
EP004	WC-4no.2	Landrace	Wollo	DZARC	—
EP005	WC-10no.75	Landrace	Wollo	DZARC	—
EP006	DW-K-Ino.24	Landrace	DZARC(Debre Zeit)	DZARC	—
EP007	DW-K-Ino.96	Landrace	DZARC(Debre Zeit)	DZARC	—
EP008	DW-K-Ino.131	Landrace	DZARC(Debre Zeit)	DZARC	—
EP009	DW-K-Ino.136	Landrace	DZARC(Debre Zeit)	DZARC	—
EP010	DW-A-Ino.71	Landrace	Akaki(Shewa)	DZARC	—
EP011	DW-A-Ino.80	Landrace	Akaki(Shewa)	DZARC	—
EP012	DW-A-Ino.130	Landrace	Akaki(Shewa)	DZARC	—
EP013	DW-A-4no.17	Landrace	Akaki(Shewa)	DZARC	—
EP014	DW-A-4no.36	Landrace	Akaki(Shewa)	DZARC	—
EP015	DW-B-3no.28	Landrace	Gojjam(Bichena)	DZARC	—
EP016	DW-B-3no.40	Landrace	Gojjam(Bichena)	DZARC	—
EP017	DW-A-3no.73	Landrace	Akaki(Shewa)	DZARC	—
EP018	CD-no.32	Landrace	USA	DZARC	—
EP019	CD-1no.65	Landrace	USA	DZARC	—
EP020	CD-1no.89	Landrace	USA	DZARC	—
EP021	DW-B1no.34	Landrace	Gojjam(Bichena)	DZARC	—
EP022	DW-B1no.98	Landrace	Gojjam(Bichena)	DZARC	—
EP023	Gojam-23no.39	Landrace	Gojjam	DZARC	—
EP024	Gojam-24no.23	Landrace	Gojjam	DZARC	—
EP025	Gojam-24no.33	Landrace	Gojjam	DZARC	—
EP026	Tigray-8no.7	Landrace	Tigray	DZARC	—
EP028	Tigray-8no.1	Landrace	Tigray	DZARC	—
EP029	Shoa-28no.15	Landrace	Shewa	DZARC	—
EP030	Shoa-28no.17	Landrace	Shewa	DZARC	—
EP031	Shoa-28no.22	Landrace	Shewa	DZARC	—
EP032	WC-1no.109	Landrace	Wollo	DZARC	—
EP033	WC-2no.1	Landrace	Wollo	DZARC	—
EP034	WC-2no.12	Landrace	Wollo	DZARC	—
EP036	WC-2no.41	Landrace	Wollo	DZARC	—
EP037	WC-2no.47	Landrace	Wollo	DZARC	—
EP038	WC-2no.58	Landrace	Wollo	DZARC	—
EP039	WC-2no.80	Landrace	Wollo	DZARC	—
EP041	WC-2no.100	Landrace	Wollo	DZARC	—
EP042	WC-4no.78	Landrace	Wollo	DZARC	—
EP043	WC-4no.85	Landrace	Wollo	DZARC	—
EP044	WC-4no.101	Landrace	Wollo	DZARC	—
EP045	WC-5no.99	Landrace	Wollo	DZARC	—

Table 1. Continued

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release
EP046	WC-6no.50	Landrace	Wollo	DZARC	—
EP047	WC-8no.57	Landrace	Wollo	DZARC	—
EP048	WC-9no.104	Landrace	Wollo	DZARC	—
EP049	WC-12no.28	Landrace	Wollo	DZARC	—
EP050	WC-12no.36	Landrace	Wollo	DZARC	—
EP051	WC-12no.40	Landrace	Wollo	DZARC	—
EP052	WC-12no.53	Landrace	Wollo	DZARC	—
EP053	WC-12no.70	Landrace	Wollo	DZARC	—
EP054	WC-14no.24	Landrace	Wollo	DZARC	—
EP055	WC-14no.29	Landrace	Wollo	DZARC	—
EP056	WC-14no.53	Landrace	Wollo	DZARC	—
EP057	WC-14no.61	Landrace	Wollo	DZARC	—
EP058	WC-14no.72	Landrace	Wollo	DZARC	—
EP059	WC-15no.105	Landrace	Wollo	DZARC	—
EP060	WC-16no.57	Landrace	Wollo	DZARC	—
EP061	WC-16no.88	Landrace	Wollo	DZARC	—
EP062	DW-K-Ino.39	Landrace	DZARC(Debre Zeit)	DZARC	—
EP063	DW-K-Ino.42	Landrace	DZARC(Debre Zeit)	DZARC	—
EP064	DW-K-Ino.52	Landrace	DZARC(Debre Zeit)	DZARC	—
EP065	DW-K-Ino.63	Landrace	DZARC(Debre Zeit)	DZARC	—
EP066	DW-K-Ino.67	Landrace	DZARC(Debre Zeit)	DZARC	—
EP067	DW-K-Ino.128	Landrace	DZARC(Debre Zeit)	DZARC	—
EP068	DW-A-Ino.27	Landrace	Akaki(Shewa)	DZARC	—
EP069	DW-A-Ino.33	Landrace	Akaki(Shewa)	DZARC	—
EP070	DW-A-Ino.48	Landrace	Akaki(Shewa)	DZARC	—
EP071	DW-A-Ino.52	Landrace	Akaki(Shewa)	DZARC	—
EP072	DW-A-Ino.57	Landrace	Akaki(Shewa)	DZARC	—
EP074	DW-A-Ino.1	Landrace	Akaki(Shewa)	DZARC	—
EP075	DW-A-Ino.19	Landrace	Akaki(Shewa)	DZARC	—
EP076	DW-A-Ino.21	Landrace	Akaki(Shewa)	DZARC	—
EP077	DW-A-Ino.50	Landrace	Akaki(Shewa)	DZARC	—
EP078	DW-B-3no.22	Landrace	Gojjam(Bichena)	DZARC	—
EP079	DW-B-3no.24	Landrace	Gojjam(Bichena)	DZARC	—
EP080	DW-B-3no.30	Landrace	Gojjam(Bichena)	DZARC	—
EP081	DW-B-3no.32	Landrace	Gojjam(Bichena)	DZARC	—
EP082	DW-A-3no.38	Landrace	Akaki(Shewa)	DZARC	—
EP083	DW-A-3no.40	Landrace	Akaki(Shewa)	DZARC	—
EP084	DW-A-3no.50	Landrace	Akaki(Shewa)	DZARC	—
EP085	DW-A-3no.58	Landrace	Akaki(Shewa)	DZARC	—
EP086	DW-A-3no.60	Landrace	Akaki(Shewa)	DZARC	—
EP087	CD-1no.10	Landrace	USA	DZARC	—
EP088	CD-1no.14	Landrace	USA	DZARC	—
EP089	CD-1no.25	Landrace	USA	DZARC	—
EP090	CD-1no.36	Landrace	USA	DZARC	—

Table 1. *Continued*

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release
EP091	CD-1no.39	Landrace	USA	DZARC	—
EP092	CD-1no.55	Landrace	USA	DZARC	—
EP093	CD-1no.58	Landrace	USA	DZARC	—
EP094	CD-1no.61	Landrace	USA	DZARC	—
EP095	Gondar-19-no.33	Landrace	Gondar	DZARC	—
EP096	CD-1no.79	Landrace	USA	DZARC	—
EP097	DW-K2no.40	Landrace	DZARC(Debre Zeit)	DZARC	—
EP098	DW-K2no.47	Landrace	DZARC(Debre Zeit)	DZARC	—
EP099	DW-K2no.60	Landrace	DZARC(Debre Zeit)	DZARC	—
EP100	Gojam-23no.3	Landrace	Gojjam	DZARC	—
EP101	Gojam-24no.31	Landrace	Gojjam	DZARC	—
EP102	Selam	Variety	DZARC(Debre Zeit)	DZARC	2004
EP103	Asassa	Variety	DZARC(Debre Zeit)	DZARC	1997
EP104	Megenagna	Variety	DZARC(Debre Zeit)	DZARC	2004
EP105	Werer	Variety	DZARC(Debre Zeit)	DZARC	2009
EP106	Mettaya	Variety	DZARC(Debre Zeit)	DZARC	2004
EP107	Ejersa	Variety	SARC(Bale)	SARC	2005
EP108	Flakit	Variety	DZARC(Debre Zeit)	DZARC	2007
EP109	Ude	Variety	DZARC(Debre Zeit)	DZARC	2002
EP110	Malefia	Variety	DZARC(Debre Zeit)	DZARC	2005
EP111	Quamy	Variety	DZARC(Debre Zeit)	DZARC	1996
EP112	Mossobo	Variety	DZARC(Debre Zeit)	DZARC	2004
EP113	Ginchi	Variety	DZARC(Debre Zeit)	DZARC	2000
EP114	Toltu	Variety	SARC(Bale)	SARC	2010
EP115	Yerer	Variety	DZARC(Debre Zeit)	DZARC	2004
EP116	Obsa	Variety	SARC(Bale)	SARC	2006
EP117	Bichena	Variety	DZARC(Debre Zeit)	DZARC	1995
EP118	Leliso	Variety	SARC(Bale)	SARC	2002
EP119	Denbi	Variety	DZARC(Debre Zeit)	DZARC	2009
EP120	Tate	Variety	SARC(Bale)	SARC	2009
EP121	Hitosa	Variety	DZARC(Debre Zeit)	DZARC	2009
EP122	Bakalcha	Variety	SARC(Bale)	SARC	2005
EP123	Kilinto	Variety	DZARC(Debre Zeit)	DZARC	1994
EP124	Oda	Variety	SARC(Bale)	SARC	2004
EP125	Kokate	Variety	DZARC(Debre Zeit)	DZARC	2005
EP126	Ilani	Variety	SARC(Bale)	SARC	2004
EP127	2000/01population69-47FRno.75	Landrace	SARC(Bale)	SARC	—
EP128	2000/01population69-47FRno.83	Landrace	SARC(Bale)	SARC	—
EP129	2000/01population69-47FRno.93	Landrace	SARC(Bale)	SARC	—
EP130	2000/01population69-47FRno.95	Landrace	SARC(Bale)	SARC	—
EP131	2000/01population69-47FRno.99	Landrace	SARC(Bale)	SARC	—
EP132	2000/01population69-47FRno.101	Landrace	SARC(Bale)	SARC	—
EP133	2000/01population69-47FRno.102	Landrace	SARC(Bale)	SARC	—
EP134	2000/01population69-47FRno.103	Landrace	SARC(Bale)	SARC	—

Table 1. *Continued*

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release
EP135	2000/01populationFRno.11	Landrace	SARC(Bale)	SARC	—
EP136	2000/01populationFRno.16	Landrace	SARC(Bale)	SARC	—
EP137	2000/01populationFRno.29	Landrace	SARC(Bale)	SARC	—
EP138	2000/01populationFRno.30	Landrace	SARC(Bale)	SARC	—
EP139	2000/01populationFRno.40	Landrace	SARC(Bale)	SARC	—
EP140	2000/01populationFRno.43	Landrace	SARC(Bale)	SARC	—
EP141	2000/01populationFRno.45	Landrace	SARC(Bale)	SARC	—
EP142	2000/01populationFRno.85	Landrace	SARC(Bale)	SARC	—
EP143	2000/01populationFRno.87	Landrace	SARC(Bale)	SARC	—
EP144	2000/01populationFRno.88	Landrace	SARC(Bale)	SARC	—
EP145	2000/01population75-51FRno.92	Landrace	SARC(Bale)	SARC	—
EP146	2000/01population75-51FRno.15	Landrace	SARC(Bale)	SARC	—
EP147	2000/01population75-51FRno.23	Landrace	SARC(Bale)	SARC	—
EP149	2000/01population75-51FRno.41	Landrace	SARC(Bale)	SARC	—
EP150	2000/01population75-51FRno.51	Landrace	SARC(Bale)	SARC	—
EP151	2000/01population75-51FRno.57	Landrace	SARC(Bale)	SARC	—
EP152	2000/01population90FRno.59	Landrace	SARC(Bale)	SARC	—
EP153	2000/01population75-51FRno.92	Landrace	SARC(Bale)	SARC	—
EP154	2000/01population37-30BDIno.7	Landrace	SARC(Bale)	SARC	—
EP155	2000/01population37-30BDIno.10	Landrace	SARC(Bale)	SARC	—
EP156	2000/01population37-30BDIno.12	Landrace	SARC(Bale)	SARC	—
EP157	2000/01population37-30BDIno.20	Landrace	SARC(Bale)	SARC	—
EP158	2000/01population37-30BDIno.26	Landrace	SARC(Bale)	SARC	—
EP159	2000/01population37-30BDIno.36	Landrace	SARC(Bale)	SARC	—
EP160	2000/01population37-30BDIno.51	Landrace	SARC(Bale)	SARC	—
EP162	2000/01population37-30BDIno.55	Landrace	SARC(Bale)	SARC	—
EP163	2000/01population37-30BDIno.63	Landrace	SARC(Bale)	SARC	—
EP164	2000/01population37-30BDIno.105	Landrace	SARC(Bale)	SARC	—
EP165	2000/01population14no.3	Landrace	SARC(Bale)	SARC	—
EP166	2000/01population14no.5	Landrace	SARC(Bale)	SARC	—
EP167	2000/01population14no.10	Landrace	SARC(Bale)	SARC	—
EP168	2000/01population14no.13	Landrace	SARC(Bale)	SARC	—
EP169	2000/01population14no.36	Landrace	SARC(Bale)	SARC	—
EP170	2000/01population14no.45	Landrace	SARC(Bale)	SARC	—
EP171	2000/01population14no.55	Landrace	SARC(Bale)	SARC	—
EP172	2000/01population14no.60	Landrace	SARC(Bale)	SARC	—
EP173	2000/01population14no.81	Landrace	SARC(Bale)	SARC	—
EP174	2000/01population14no.94	Landrace	SARC(Bale)	SARC	—
EP175	2000/01population14no.106	Landrace	SARC(Bale)	SARC	—
EP176	2000/01population25-23BDIno.1	Landrace	SARC(Bale)	SARC	—
EP179	2000/01population25-23BDIno.18	Landrace	SARC(Bale)	SARC	—
EP180	2000/01population25-23BDIno.22	Landrace	SARC(Bale)	SARC	—
EP181	2000/01population25-23BDIno.24	Landrace	SARC(Bale)	SARC	—
EP182	2000/01population25-23BDIno.27	Landrace	SARC(Bale)	SARC	—

Table 1. *Continued*

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release
EP183	2000/01population25-23BDIno.29	Landrace	SARC(Bale)	SARC	—
EP184	2000/01population25-23BDIno.35	Landrace	SARC(Bale)	SARC	—
EP185	2000/01population25-23BDIno.42	Landrace	SARC(Bale)	SARC	—
EP186	2000/01population25-23BDIno.45	Landrace	SARC(Bale)	SARC	—
EP187	2000/01population25-23BDIno.48	Landrace	SARC(Bale)	SARC	—
EP188	2000/01population25-23BDIno.50	Landrace	SARC(Bale)	SARC	—
EP189	2000/01population25-23BDIno.57	Landrace	SARC(Bale)	SARC	—
EP190	2000/01population25-23BDIno.60	Landrace	SARC(Bale)	SARC	—
EP191	2000/01population25-23BDIno.64	Landrace	SARC(Bale)	SARC	—
EP192	2000/01population25-23BDIno.68	Landrace	SARC(Bale)	SARC	—
EP193	2000/01population25-23BDIno.72	Landrace	SARC(Bale)	SARC	—
EP194	2000/01population25-23BDIno.80	Landrace	SARC(Bale)	SARC	—
EP195	2000/01population25-23BDIno.83	Landrace	SARC(Bale)	SARC	—
EP196	2000/01population25-23BDIno.90	Landrace	SARC(Bale)	SARC	—
EP197	2000/01population25-23BDIno.93	Landrace	SARC(Bale)	SARC	—
EP198	2000/01population25-23BDIno.105	Landrace	SARC(Bale)	SARC	—
EP199	2000/02population82no.4	Landrace	SARC(Bale)	SARC	—
EP200	2000/02population82no.5	Landrace	SARC(Bale)	SARC	—

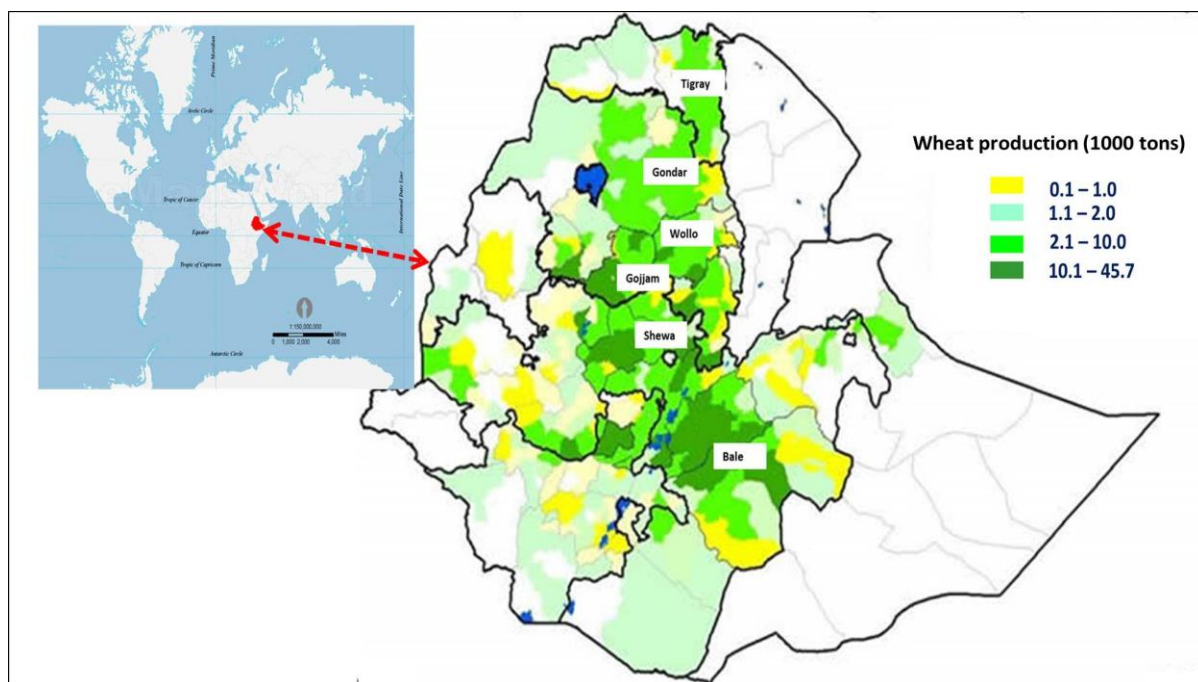


Figure 4. Map of Ethiopia showing major wheat producing areas from where 167 landraces were originally collected. (Source: Atlas of the Ethiopian rural Economy (2006); <http://www.ifpri.org/node/3763>).

3.1.2. DNA Extraction and SNP Genotyping

A pooled tissue sample of twenty five one-week-old seedlings were taken for genomic DNA extraction for each accessions. DNA extraction was done with DNeasy 96 Plant Kit (Qiagen GmbH, Hilden, Germany) according to the kit protocol. Briefly, the leaf samples were mechanically disrupted followed by chemical lyses. The cell debris, precipitated proteins as well as polysaccharides were removed by centrifugation while RNA was removed by RNase during lysis. Lysates were then loaded onto the DNeasy plant 96-well plates after adjusting the buffering conditions. During the spinning, while DNA selectively binds to the silica, membrane contaminants were passed through and finally, pure DNA was eluted in water.

SNP markers were generated using the Illumina iSelect® 90K wheat SNP assay comprising 81,587 gene-associated SNPs (Wang *et al.*, 2014). Marker genotypes were called with the GenomeStudio v2011.1 software package (Illumina, San Diego, CA, USA) as described in Cavanagh *et al.* (2013). In brief, the default clustering algorithm implemented in Genome Studio was first used to identify assays that produced three distinct clusters corresponding to the AA, AB and BB genotypes expected for biallelic SNPs. Manual curation was performed for assays that produced compressed SNP allele clusters that could not be discriminated by the default algorithm. The accuracy for SNP clustering was validated visually.

Calls showing residual heterozygosity were entered as missing values before exporting genotype data from GenomeStudio. A high-density consensus map of tetraploid wheat generated by Maccaferri *et al.* (2015) was used to know chromosome positions of SNPs.

3.1.3. Genetic Diversity Analysis

Numbers and percent of polymorphic loci, polymorphism information content (PIC), Nei's gene diversity and minor allelic frequency (MAF) were calculated using Power Marker v 3.25 (Liu and Muse, 2005). Principal component analysis (PCA) (Price *et al.*, 2006) for the genetic relationships among individuals was calculated using a package "SNPrelate" (Zheng, 2012) in R studio (R Development Core Team, 2013). Neighbor-Joining tree based on simple matching dissimilarity coefficient was constructed using DARwin var. 6.0.14 (Perrier and Jacquemoud-Collet, 2006) and the resulting trees were displayed using FigTree var. 1.4.3 (Andrew, 2016). A software package Arlequin v.3.5.2.2 (Excoffier *et al.*, 2005) was used to assess the molecular

variance (AMOVA) between clusters based on the inferred subpopulations and between landraces and varieties.

3.1.4. Linkage Disequilibrium (LD) Analysis

Linkage disequilibrium (LD) was calculated as r^2 values between pairwise SNPs using TASSEL v.5.2 (Bradbury *et al*, 2007). LD was calculated for each chromosomes, genomes and whole genome. The specific critical r^2 value beyond which LD is due to true physical linkage was determined by taking the 95th percentile of r^2 data of unlinked marker pairs (Brescaglio and Sorrells, 2006). Linkage Disequilibrium decay was analyzed as per physical distance using the procedure of Hill and Weir (1988) in R environment (R Development Core Team, 2013) and LD decay curve was fitted by a smoothing spline regression line at the genome level.

3.1.5. Population Structure and Kinship Analysis

Two approaches were implemented to infer the optimal clusters/sub-populations existed in 192 Ethiopian durum wheat accessions. The first approach was based on a Bayesian model-based (Markov Chain Monte Carlo) clustering approach implemented in STRUCTURE v.2.3 software package (Pritchard *et al.*, 2000). The Haploview Tagger function (based on analysis of marker pairwise r^2 values) was used to select a tag-SNPs for population structure analysis with a tagger filter set at $r^2 = 0.5$ in HAPLOVIEW v4.2 (Barrett *et al.*, 2005) and 1,496 tag-SNPs were selected and used for population structure analysis. To infer the optimal sub-populations, an ad hoc quantity (ΔK) approach was used that is calculated based on the second order rate of change of the likelihood (ΔK) (Evanno *et al.*, 2005) and in this analysis approach, the ΔK shows a clear peak at the ideal number of sub-populations. To perform this, 10

sub-populations with 20 independent iterations for each sub-population was done under admixture model of population structure with correlated allele frequencies and 50,000 lengths burn-in period and 100,000 Markov Chain Monte Carlo (MCMC) replications after burn-in were applied for each iteration.

The second approach was based on the discriminant analysis of principal components (DAPC), which was implemented using a package “adeigenet” (Jombart *et al.*, 2010) in R studio. In this method, ideally, the optimal clustering solution should correspond to the lowest Bayesian Information Criterion (BIC) and the number of clusters determined as the value of k above which BIC values decreased spontaneously.

The Haploview Tagger function was also used to select a tag-SNPs for kinship matrix (K) analysis with a tagger filter set at $r^2 = 1$ in HAPLOWVIEW v4.2 (Barrett *et al.*, 2005) and 4,842 tag-SNPs were selected to calculate the kinship similarity matrix.

3.2. Genome-Wide Association Analysis for Seminal Root System Architecture Traits

3.2.1. Plant Materials

The same accessions as characterized for genetic diversity analysis (section 3.1, Table 1) were assembled for genome-wide association (GWAS) analysis of root system architecture (RSA) traits.

3.2.2. Root System Architecture Phenotyping

Seminal RSA traits were characterized using the protocol described by Cane *et al.* (2014) and later used by Maccaferri *et al.* (2016) with some minor modifications in

the present work. For each accession, 60 seeds were first weighed to collect data for the initial thousand grain weight (iTGW) that was later used as a covariate for the QTL analysis in order to eliminate the possible effect from seed size. Later, 20 seeds were sterilized in 0.15% panoptine solution and dried before pre-germinating in Petri dishes with wet filter paper at 28 °C for 24 h. Then, five homogeneous seeds with homogenous seminal root emission were positioned 7 cm apart on a distilled-water-wet filter paper sheet placed on a vertical black rectangular (42.5 × 38.5 cm) polycarbonate plate for root obscuration. Distilled water was used for growth of plantlets.

Root System Architecture traits were then measured in plantlets that were grown for 12 days at 22 °C (day)/18 °C (night) under a 16-h photoperiod and light intensity of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR). The experiment was conducted through a randomized complete block design (RCBD), with three independent replications, which were grown consecutively in the same growth chamber. The experimental unit was equal to a 0.16 m² area of screening plate having five homogenous seedlings of the same genotype and hence one screening plate corresponded to one genotype. Blocking was introduced to control for possible differences in growth rate. Due to the high number of genotypes under evaluation coupled with the time required for root preparation and root image acquisition, genotypes were divided into sets of 25–30 accessions that were considered as blocks. Blocks were corresponded to accessions phenotyped on the same date and kept on shelves in the growth chamber that are positioned at the same distance from the floor under uniform light conditions (see **Figure 5**). Normalization of the blocking effect (linear adjustment) was undertaken in the ANOVA.

Data for the following RSA traits were taken based on single-plantlet basis: root growth angle (RGA) was measured as the linear distance between the two most external seminal roots of each plantlet at 3.5 cm from the seed tip and then converted to degrees (**Figure 6**). Total root length (TRL); Average root length (ARL); Total root number (TRN); the presence of 6th seminal root (RT6) were recorded. Bulk roots and shoots from each experiment were cut and dried to determine the root dry weight (RDW) and shoot dry weight (SDW) for each replicate. Total root length and root growth angle were measured on plantlets' images using GIMP (GNU Image Manipulation Program) and ImageJ (Collins, 2007). Average root length was estimated as total root length divided by total root number. Individual root dry weight (IRW) was derived from the result of the bulked root dry weight divided by the total root number and could be used as a proxy to measure root thickness.

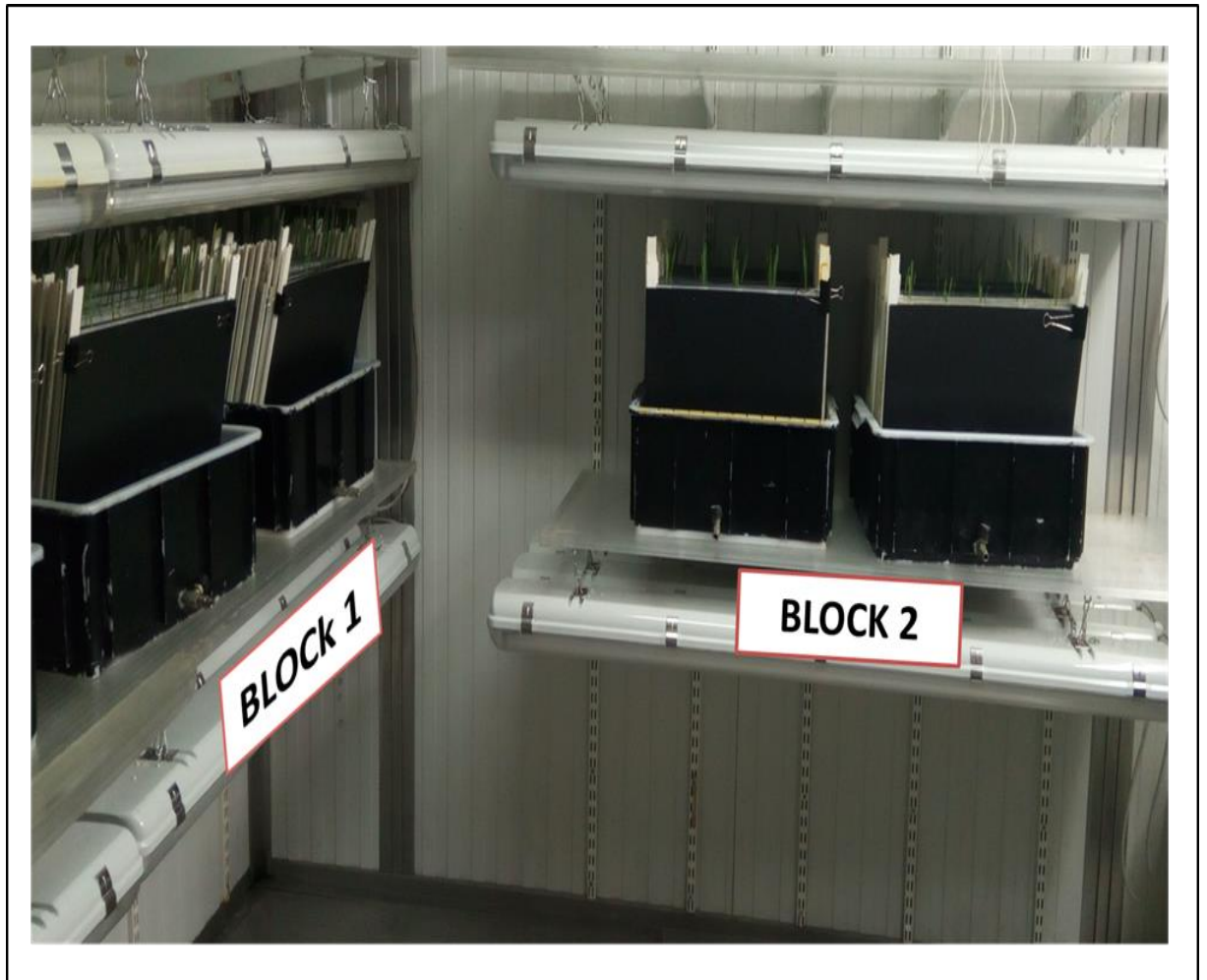


Figure 5. Introduced blocks during the root experiment at the growth chamber that includes accessions phenotyped at the same date and put on shelves positioned at the same distance from the floor under uniform light conditions.

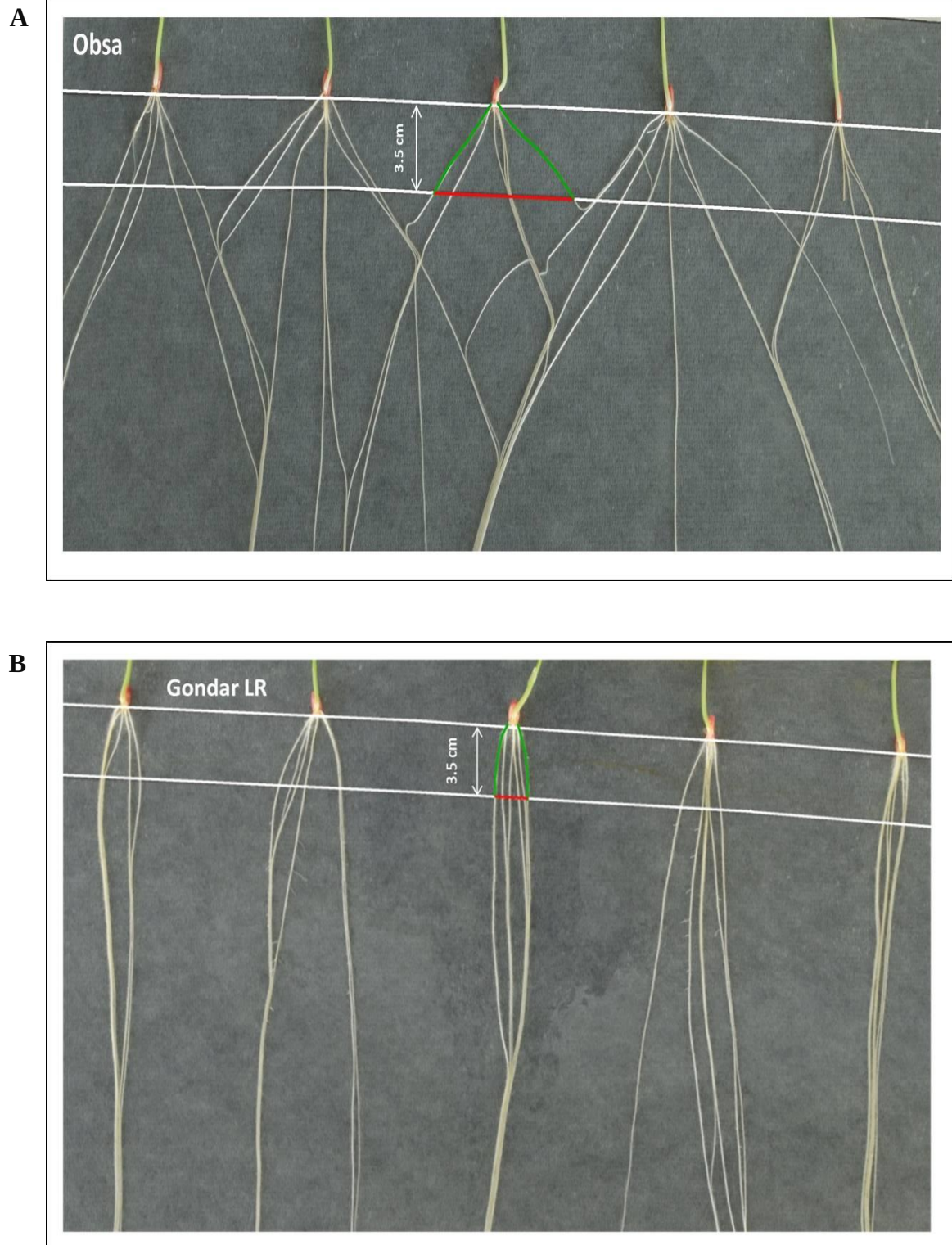


Figure 6. Root growth angle (RGA) of seminal roots for 12-day-old seedlings of Obsa variety (with wide angle) and Gondar landrace (with narrow angle) measured as the linear distance (red) of the two most external roots (green) distant 3.5 cm from the tip of the seed and later converted into degree.

3.2.3. Phenotypic Data Analysis

Analysis of variance (ANOVA) was conducted for all RSA traits including blocks, replications, and accessions. Block effect was controlled by taking the mean of each set of genotypes included in the same block and used to correct the corresponding single values, whenever significant, with a linear regression method. The grain weight of the seeds (iTGW) used in the root experiments was also treated as a covariate to correct for any possible variation caused by seed weight. In addition, the trait was also subjected to GWAS analysis along with other RSA traits.

Broad-sense heritability (H^2) of RSA traits was calculated with the mean values of each experiment among the three replications according to Lynch and Walsh (1998).

$$H^2 = \sigma_G^2 / \sigma_G^2 + \sigma_E^2$$

Where σ_G^2 (genetic variance) was calculated as $(MS_{\text{genotypes}} - MS_{\text{residual}})/r$; σ_E^2 (the residual variance) = MS_{residual} ; r is the number of replications and MS is the mean square value. The coefficient of variance (CV) was calculated for all RSA traits except for the presence of the 6th root (since it is a trait with discrete values). The CV was calculated as the division values of standard deviation over a mean ($CV = \sigma/\mu$).

3.2.4. Genotypic Data

The same source of genomic data used for genetic diversity analysis (section 3.1.2) applied for RSA-GWAS analysis. Similar seed source was used for RSA phenotypic evaluation. SNP markers with < 0.05 minor allele frequencies (MAF) and markers with > 0.1 missing values per accession were excluded. Imputation of the missing data was computed using Beagle 4.0 (Browning and Browning, 2007). Finally, after

filtering and imputation, 10,789 polymorphic SNP markers (4,591 and 6,198 SNPs from A and B genomes, respectively) were used for RSA-GWAS analysis.

3.2.5. GWAS Analysis

In order to control the false-positive associations, a mixed linear model (MLM) (Yu *et al.*, 2005) with population structure (*Q*) and kinship (*K*) covariates was applied for the GWAS analyses. All 10,789 polymorphic SNP markers (4,591 SNPs from A and 6,198 SNPs from B genomes) and phenotypic data of RSA traits generated from 192 Ethiopian durum wheat accessions along with covariates were used to conduct the marker-trait association (MTA) analysis. Three levels of significance were introduced according to Maccaferri *et al.* (2016) for reporting the GWAS-QTLs: (i) experiment-wise $P \leq 0.05$ ($-\log_{10} P \geq 4.00$) for "major QTLs"; (ii) marker-wise $P \leq 0.001$ ($-\log_{10} P \geq 3.00$) for "nominal QTLs"; (iii) marker-wise $P \leq 0.01$, ($-\log_{10} P \geq 2.00$) for "suggestive QTLs". The experiment-wise threshold was projected according to the number of 'independent SNP tests' that was estimated in HAPLOWVIEW v4.2 (Barrett *et al.*, 2005) using the tagger function of $r^2 = 0.3$ (Carlson *et al.*, 2004) and total number of tag-SNPs was equal to 816. Bonferroni adjustment for multiple GWAS tests ($P \leq 0.05$) was equal to $-\log_{10} P = 4.21$ (rounded to 4). Hence the experiment-wise, Bonferroni-corrected significance threshold at $P = 0.05$ matched to a marker-wise threshold of $-\log_{10} P \geq 4.00$.

Significance intervals of identified QTLs were reported as the intervals after including all SNPs associated with the trait with $P \leq 0.01$ (marker-wise) and in LD of $r^2 \geq 0.3$. Confidence intervals were defined based on the GWAS-QTL peak ± 2.25 cM on both map sides.

The relative positions of RSA QTLs identified in this study along with other previous studies (An *et al.*, 2006; Laperche *et al.*, 2006; Kubo *et al.*, 2007; Guo *et al.*, 2012; Hamada *et al.*, 2012; Bai *et al.*, 2013; Christopher *et al.*, 2013; Liu *et al.*, 2013; Cao *et al.*, 2014; Atkinson *et al.*, 2015; Petrarulo *et al.*, 2015; Maccaferri *et al.*, 2016; Iannucci *et al.*, 2017) were compared based on the projected QTL peaks and confidence intervals on the tetraploid consensus map (Maccaferri *et al.*, 2015).

3.3. Genome-Wide Association Mapping for Grain Shape and Color Related Traits

3.3.1. Plant Materials

The same accessions as characterized for genetic diversity analysis (section 3.1, Table 1) were assembled for GWAS analysis of grain shape and color related traits.

3.3.2. Phenotypic Data

All landrace accessions and varieties were planted for two consecutive main seasons at Sinana Agricultural Research Center (SARC) for homogeneity and purification using ear-to-row planting method. The field was managed following the local normal agricultural practices. Seeds harvested at the second year were used to measure grain shape and grain color traits. Sixty homogenous and healthy seeds were selected from each accession for digital image analysis. Digital images were acquired with a flatbed CanoScan LiDE 120 F (Canon Inc, Tokyo, Japan), with a true optical resolution of 4800 dpi and 48-bit internal color depth. Seeds were spread on the scanner glass carefully and homogeneously spaced for accurate measurement. A black cardboard was used to cover the scanner to increase the contrast and decrease reflection. All images were scanned at 24-bit with 300 dpi resolution and 2250 × 3705 pixel and recorded in a JPEG format labeling with their respective accession name.

3.3.3. Digital Image Analysis

The digital image measurement was done with a software package GrainScan (Whan *et al.*, 2014) which is developed for a high-throughput phenotyping of cereal grains. The default-automated threshold was used to measure grain length (GL) (mm) and grain width (GW) (mm). The mean value of 60 homogeneous seeds was taken for each trait. CIE (Commission Internationale l'Eclairage) Lab, a three-dimensional (L*a*b*) color space method, was used to measure the color of accessions. Calibration with a color checker, which is scanned under the same setting as the seeds, was used to change the raw RGB value measured by the scanner to a standardized CIE L*a*b* values. CIE L* values represent brightness, CIE a* indicates redness (+ve values) and greenness (-ve values) and CIE b* represent yellowness (+ve value) and blueness (-ve value).

3.3.4. Phenotypic Data Analysis

Minitab 18 software package was used for the analysis of one-way ANOVA and other descriptive statistics with the accessions mean values of seed weight, shape and color-related traits. Pearson's correlation was conducted between the studied traits.

3.3.5. Genotypic Data and GWAS Analysis

A similar genotypic data source (explained in section 3.2.4) and GWAS analysis method (explained in section 3.2.5) was applied for detecting QTLs linked with grain shape and color related traits.

4. RESULTS

4.1. Genetic Diversity, Linkage Disequilibrium and Population Structure

4.1.1. SNP Markers Distribution

From 81,587 SNP probes available on the chip, 30,510 SNP calls (7,156 monomorphic and 23,354 polymorphic SNPs) were reproducible in the current panel. From these markers, 18,788 SNPs (3,736 monomorphic and 15,338 polymorphic SNPs) had a known position and only 15,338 polymorphic SNPs were used for the current genetic diversity analysis. The smallest SNP markers were recorded on chromosome 1A (263 SNPs) while the highest on chromosome 2B (2,253 SNPs) (**Table 2**). Chromosome 2B also contributed the highest polymorphic SNP markers (1,755 SNPs) while lowest number of polymorphic SNPs were on chromosome 1A (236 SNPs). When considering the distribution of SNPs across homoeologous chromosomes, group two scored highest numbers of SNP markers (3,639 SNPs) and lowest number on group one (1,709 SNPs). Higher Polymorphic SNP markers were recorded on B genome (11,084 SNPs) than A genome (7,704 SNPs) in Ethiopian durum wheat accessions.

4.1.2. Genetic Diversity Analysis

The SNP markers showed a wide range of polymorphic information content (PIC) and Nei's gene diversity of the panel across chromosomes and genomes. Frequency distribution of SNPs for PIC, gene diversity and frequency of the minor allele (MAF) values on the whole genome is presented in **Figure 7**, while details of the frequency distribution of SNP markers on each chromosome is presented for values of gene diversity (**Appendix Figure 1**), PIC (**Appendix Figure 2**) and minor allelic frequency

(**Appendix Figure 3**). The overall mean values of polymorphic information content (PIC) was 0.202 with a range score of 0.01 to 0.375. Nei's gene diversity varied from 0.01 to 0.5 with the whole genome mean values of 0.246. The mean MAF of the genome was 0.175 with a minimum and maximum scores of 0.005 to 0.5, respectively. Chromosome 2A scored the highest PIC and gene diversity of 0.229 and 0.282, respectively (**Table 3**). In contrast, the lowest PIC and genetic diversity were observed on chromosome 7A with the values of 0.181 and 0.217, respectively. Chromosomes 2A, 2B, 3A, 3B, 7A and 7B showed slightly lower polymorphic information content value than the average PIC values of the whole genome. On the other hand, homoeologous chromosome groups 1, 4, 5 and chromosome 6A scored higher Nei's genetic diversity than the average Genome-wide value. The highest gene diversity, PIC and MAF were on homoeologous group five. Comparable mean values of genetic diversity, PIC and MAF were scored on A and B genomes.

Table 2. Distribution of SNPs generated from the 90K Illumina iSelect SNPs array across chromosomes in 192 Ethiopian durum wheat panel.

Chromosomes	No. of Polymorphic SNPs	No. of Monomorphic SNPs	Total SNPs
A-Genome			
1A	236	27	263
2A	1,097	289	1,386
3A	909	219	1,128
4A	831	166	997
5A	895	238	1,133
6A	1,100	190	1,290
7A	1,257	250	1,507
B-Genome			
1B	1,207	239	1,446
2B	1,755	498	2,253
3B	1,203	359	1,562
4B	894	135	1,029
5B	1,416	263	1,679
6B	1,249	304	1,553
7B	1,289	273	1,562
Homoeologous			
1	1,443	270	1,709
2	2,852	783	3,639
3	2,112	860	2,690
4	1,725	305	2,026
5	2,311	507	2,812
6	2,349	506	2,843
7	2,546	505	3,069
A-Genome	6,325	1,379	7,704
B-Genome	9,013	2,071	11,084
Whole Genome	15,338	3,450	18,788

4.1.3. Linkage Disequilibrium

Genome-wide linkage disequilibrium (LD) was estimated by taking the pairwise r^2 values of SNP markers. The mean r^2 of the whole genome was 0.12, of which 55 % of the pair-wise LD comparisons were significant at $P < 0.01$. Chromosome 3B scored the highest mean values of r^2 (0.19) with 64 % of pair-wise LD comparisons were significant. On the other hand, 7A scored the lowest mean r^2 values (0.108) and 48 % of pairwise LD comparisons were significant (**Table 5**).

The genome-wide LD decay of the panel indicated that LD decayed below $r^2 = 0.3$ (the standard critical threshold) at 2.25 cM (**Figure 8**). This specifies ± 2.25 cM would be the significant interval of a particular QTL from the QTL-tag SNP (a SNP found at the peak of corresponding QTL). The specific critical r^2 value of the panel beyond which LD is due to true physical linkage was 0.15 and the intersect of the threshold and the LD decay curve was at 5.75 cM.

Table 3. Mean values of diversity indices and minor allelic frequency distribution of SNP markers across chromosomes in 192 Ethiopian durum wheat accessions.

Chromosome	Nei's Gene diversity	Polymorphic information content (PIC)	Minor allelic frequency (MAF)
A-Genome			
1A	0.282	0.229	0.208
2A	0.221	0.185	0.150
3A	0.246	0.202	0.175
4A	0.248	0.204	0.176
5A	0.272	0.221	0.200
6A	0.265	0.215	0.194
7A	0.217	0.181	0.150
B-Genome			
1B	0.254	0.208	0.185
2B	0.229	0.190	0.158
3B	0.233	0.194	0.159
4B	0.279	0.226	0.209
5B	0.265	0.217	0.191
6B	0.246	0.203	0.172
7B	0.235	0.193	0.164
Homoeologous			
1	0.259	0.211	0.188
2	0.226	0.188	0.155
3	0.238	0.197	0.166
4	0.264	0.215	0.193
5	0.268	0.218	0.194
6	0.255	0.209	0.182
7	0.226	0.187	0.157
A-Genome	0.2448	0.2015	0.1744
B-Genome	0.2471	0.2035	0.1750
Whole Genome	0.2462	0.2027	0.1748

Table 4. Mean of diversity indices and minor allelic frequency distribution of SNPs in landraces and varieties of Ethiopian durum wheat.

Accession Type	Sample size	No. of polymorphic SNPs	Nei's Gene diversity	Polymorphic information content (PIC)	Minor allelic frequency (MAF)
Landrace	167	13,466	0.213	0.173	0.154
Variety	25	13,725	0.297	0.240	0.218

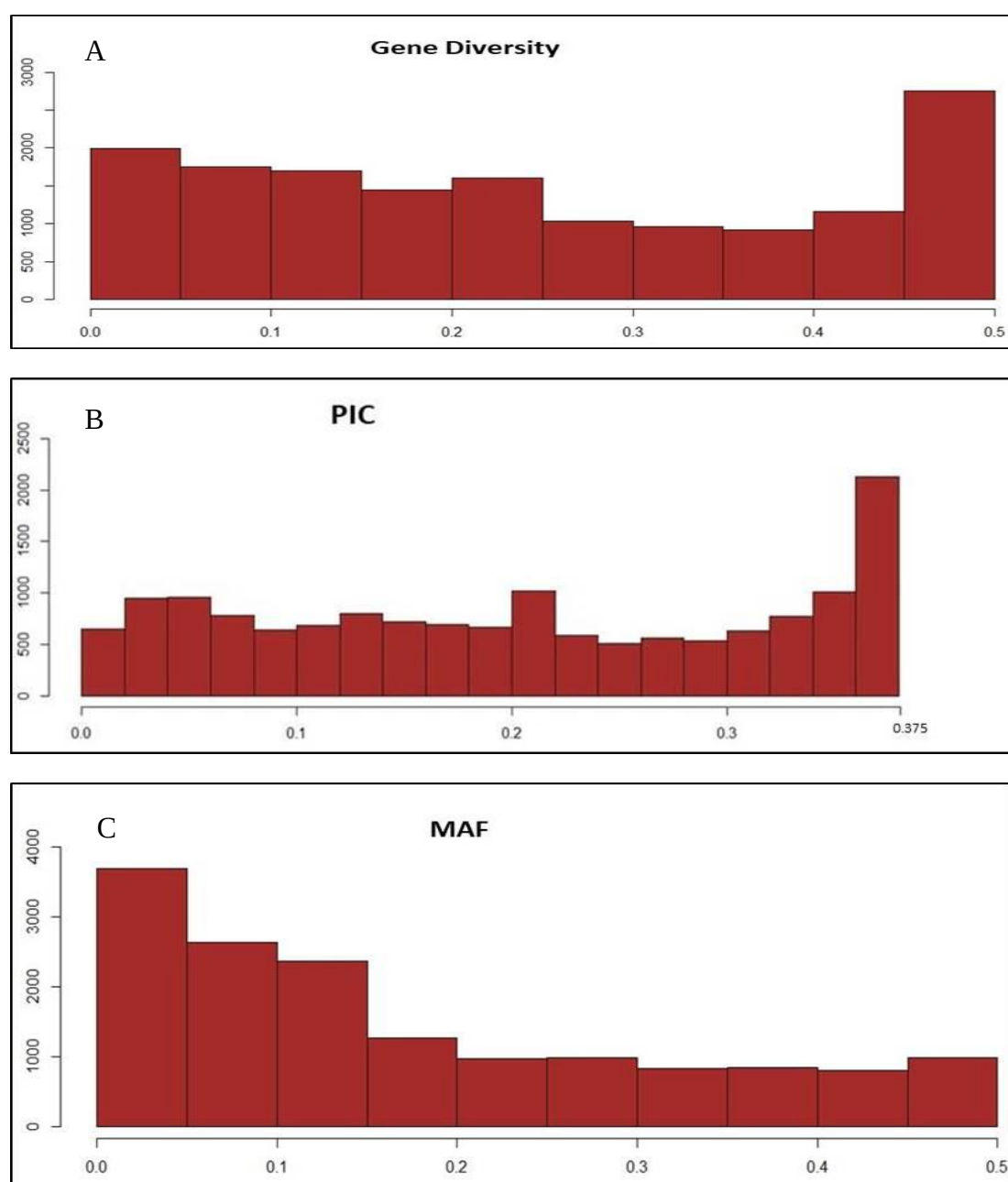


Figure 7. Frequency distribution of Nei's gene diversity (A), polymorphic information content (PIC) (B) and minor allelic frequency (C) values of 15,338 polymorphic SNPs.

Table 5. Mean value of LD (r^2) and percentage of significant ($P < 0.01$) SNP pairs in LD scored in Ethiopian durum wheat panel across chromosomes and genomes.

Chromosomes	r^2	Sig. SNP pairs in LD (%)
1A	0.1625	64.04
1B	0.1090	51.81
2A	0.1629	59.19
2B	0.1290	57.05
3A	0.1375	56.36
3B	0.1921	64.02
4A	0.1603	62.24
4B	0.1430	55.46
5A	0.1523	58.79
5B	0.1159	52.27
6A	0.1279	52.99
6B	0.1106	49.81
7A	0.1080	47.72
7B	0.1253	59.27
A genome	0.1221	55.76
B genome	0.1113	54.43
Whole Genome	0.1219	55.18

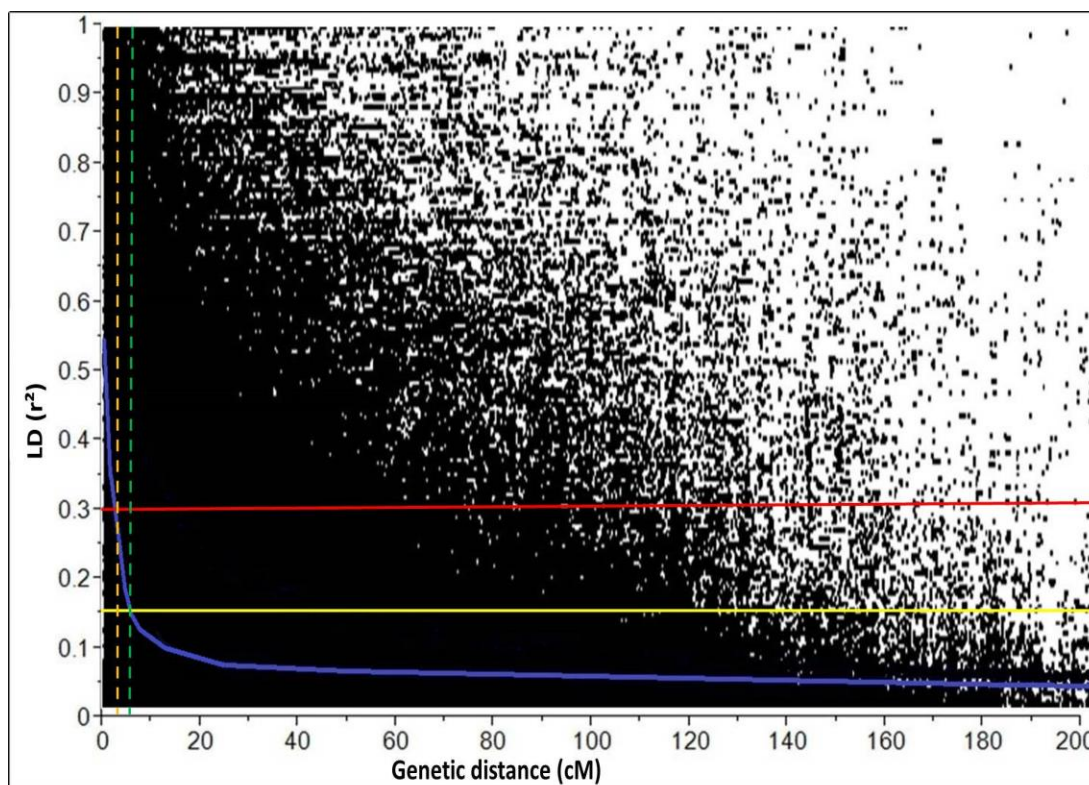


Figure 8. A scatter plot of pairwise SNPs showing genome-wide Linkage disequilibrium (LD) decay plot in 192 Ethiopian durum wheat accessions. The genetic distance in cM is plotted against the LD estimate (r^2) for pairs of markers. The blue solid curve represents the smoothing spline regression model fit to LD decay. The horizontal red solid line represents standard critical r^2 value of the genome ($r^2 = 0.30$); horizontal yellow solid line represents the 95th percentile unlinked r^2 value of the genome line ($r^2 = 0.15$); the vertical orange dash line represents the genetic distance (2.25 cM) at which the standard critical r^2 intersects with the LD decay curve; and green dash line represents the genetic distance (5.75 cM) at which the 95th percentile unlinked r^2 intersects with the LD decay curve.

4.1.4. Genetic Stratification and PCA Analysis

The optimal sub-populations of the panel were inferred through two approaches: The first method was a Bayesian model-based clustering approach that is based on the second order rate of change of the likelihood (ΔK) (**Appendix Table 2**). The result indicated a clear peak at $K = 3$ signifying the optimal sub-populations in the panel (**Figure 9A**). The second approach was based on the discriminant analysis of

principal components (DAPC) and the result couldn't show a clear lowest Bayesian information criterion (BIC) on a specific K value above which BIC values decreased spontaneously followed by simultaneous increment making an elbow at the optimal K value (**Figure 9B**). However, it provided a clue in which somehow less than 5 clusters could be optimal. Hence, accessions were grouped into 3 sub-populations (based on the result from ΔK values) with 75, 27 and 90 accessions came together for subpopulation 1, 2 and 3, respectively (**Appendix Table 1**). Landraces grouped on clusters one and three while all varieties, except one (selam) that was clustered with group one, gathered on cluster two. Heat map clustering result based on kinship matrix from 4,842 tag-SNPs using identity-by-state (IBS) algorithm showed three clear clusters (**Figure 10A**) and aligned with STRUCTURE-inferred subpopulations (**Figure 10B**). The neighbor-joining based clustering analysis (**Figure 11**) also confirmed by showing a three clear clusters and except one accession, all are grouped based on the ΔK based stratification result.

Principal component analysis (PCA) was conducted with SNPs data generated from the panel. The first, second and third principal components explained 24.29, 6.61 and 3.74 % of the total variance. The smaller numbers of variance explained by the second and consecutive PCs indicated that only few PCs couldn't encapsulate the existing genetic variation in Ethiopian durum wheat. The first PC (PC1) distantly clustered varieties from landraces and the second PC clearly grouped the two landrace subgroups (**Figure 12A**). The first two PCs (PC1 and PC2) clearly clustered the three sub-populations. However, clustering got distorted when additional principal components were considered (**Figure 12B**).

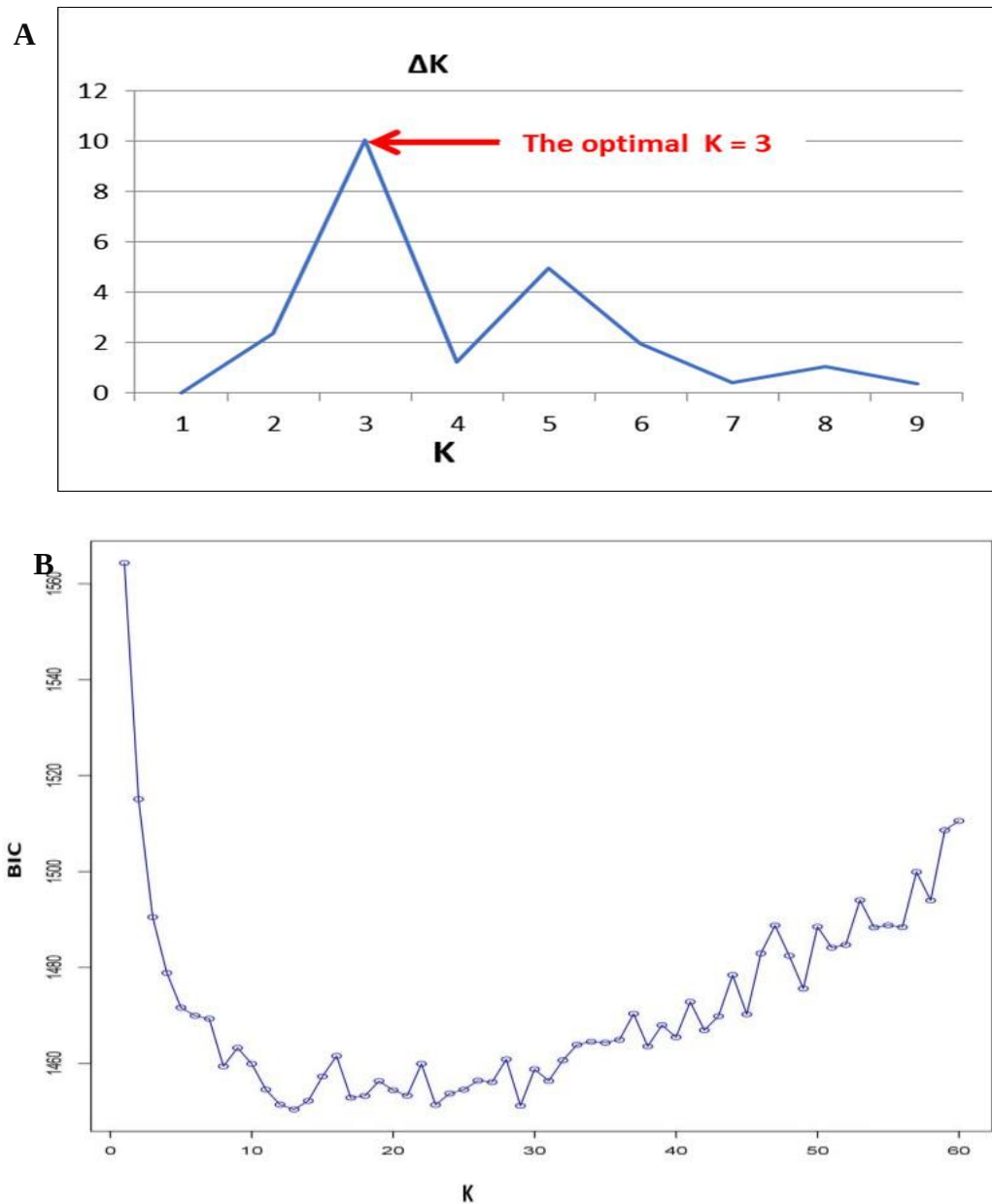


Figure 9. Inference of the optimal numbers of subpopulations in Ethiopian durum wheat panel (A) using Bayesian clustering model with ΔK value and (B) by discriminant analysis of principal components (DAPC) using adegenet package implemented in R software.

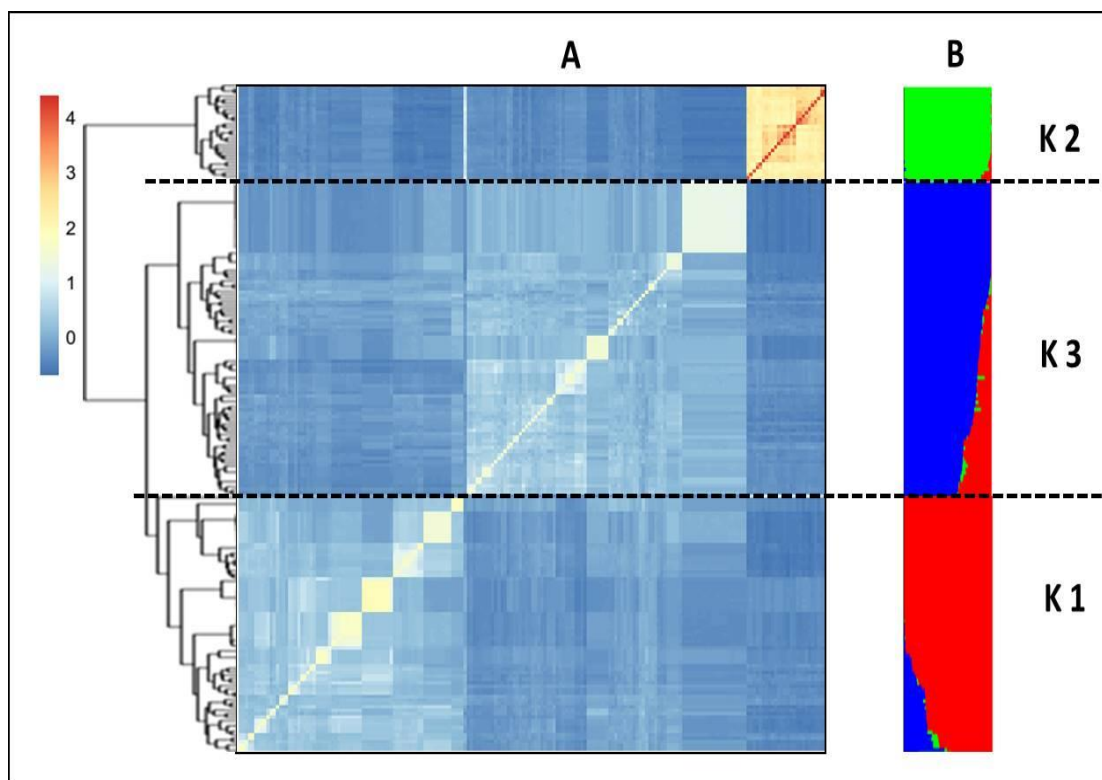


Figure 10. Population structure and kinship-matrix similarity analysis for Ethiopian durum wheat accessions. **(A)** Heat map clustering result using the kinship matrix from tag-SNP ($r^2 = 1$) by identity-by-state (IBS) algorithm. **(B)** Population structure plot and K1, K2 and K3 represents subpopulations 1, 2 and 3, respectively. The black-dash lines separated the panel into three subpopulations. Accessions arrangement was based on the order of heat map kinship result. The colored lines represent the membership of each accession in the STRUCTURE-inferred subpopulations.

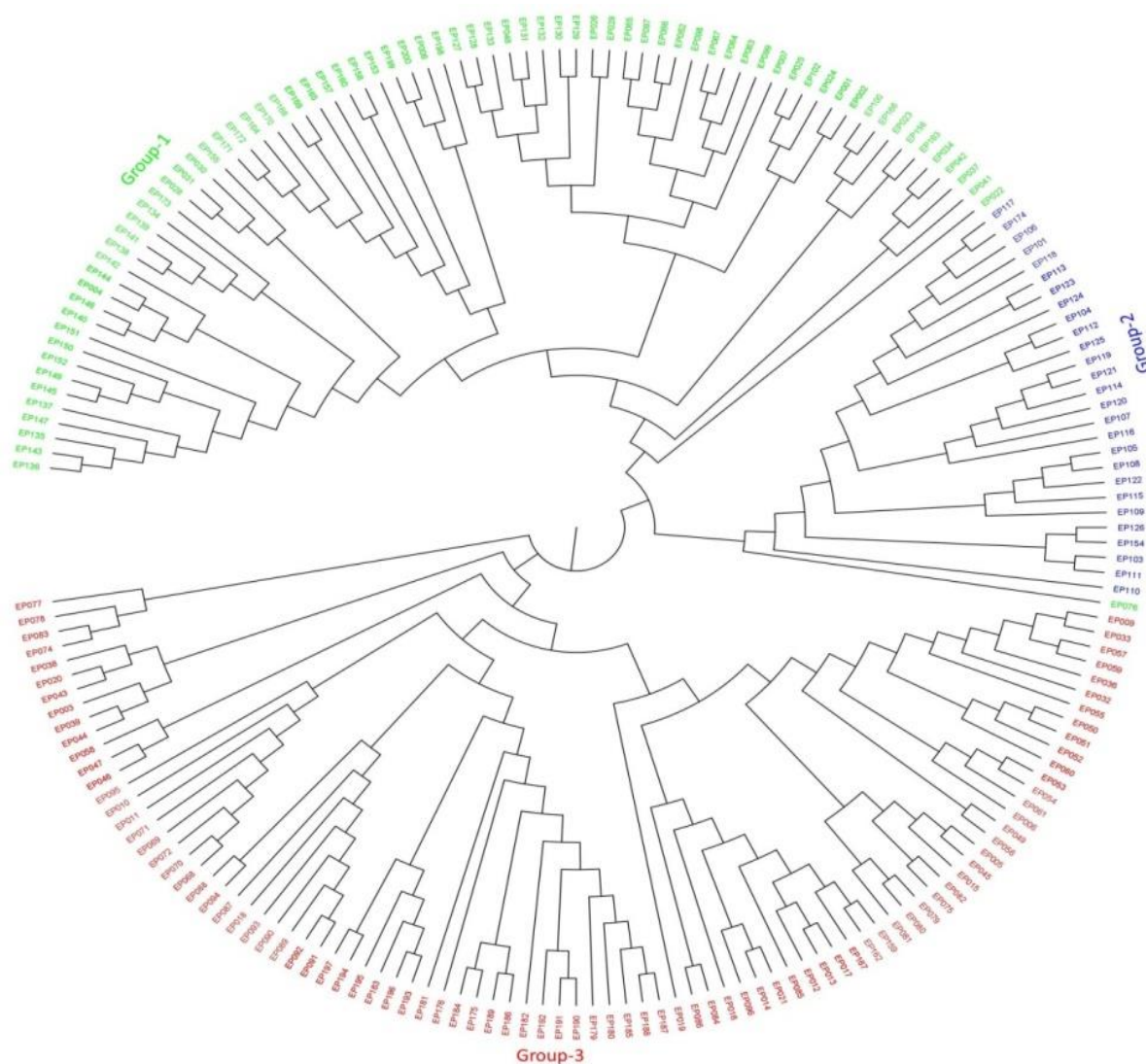


Figure 11. Neighbor-joining tree generated based on simple matching dissimilarity coefficients for 192 Ethiopian durum wheat accessions based on SNP markers. Color of accessions were based on clusters inferred from population structure ΔK based analysis .

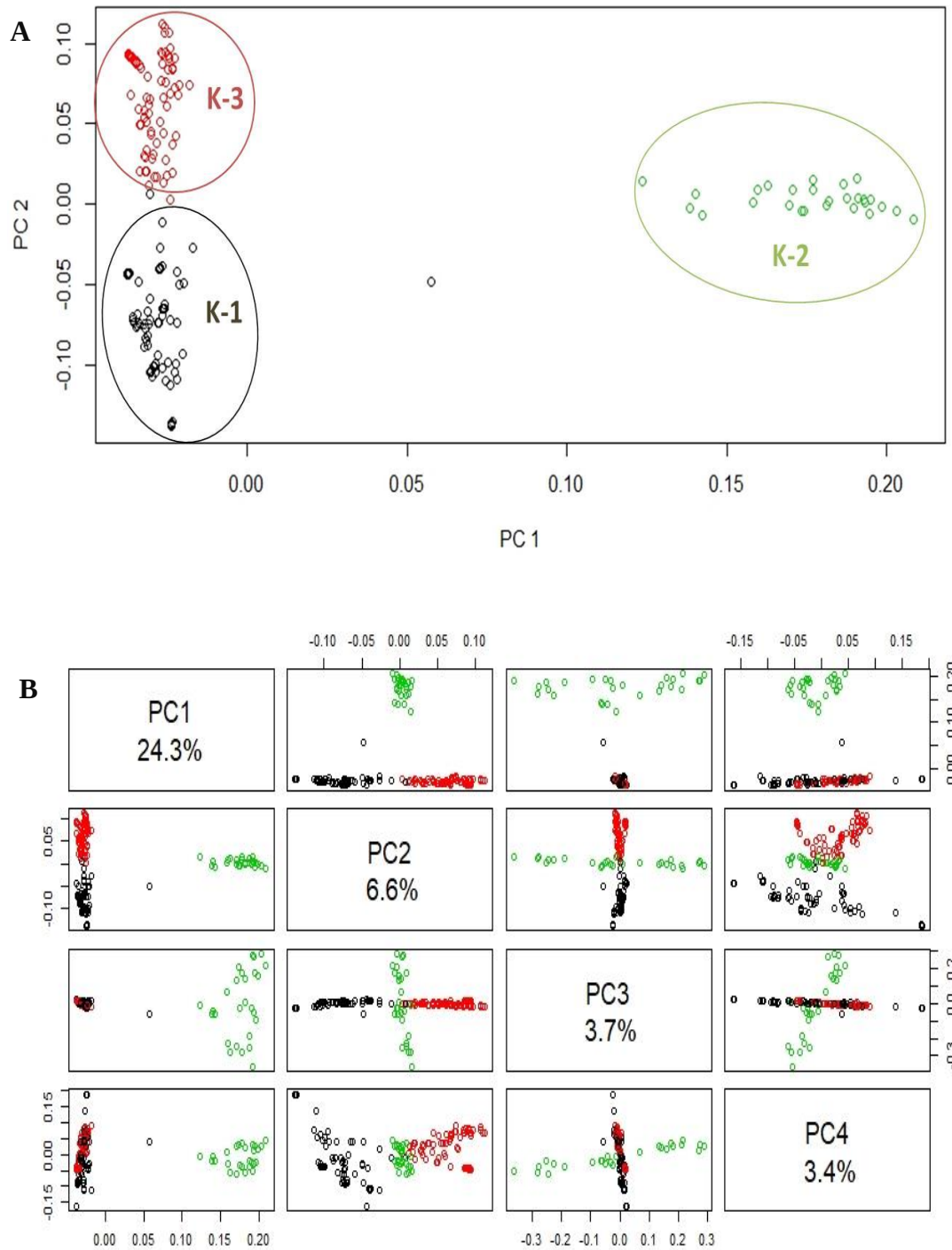


Figure 12. Principal component analysis (PCA) using 15,338 polymorphic SNP markers generated from 192 Ethiopian durum wheat accessions. Varieties cluster (green, K-2) showed a clear separation from the other two landrace clusters (K1 & K2) using PC1 and PC2 (A). Clustering got disrupted when considering other PCs (B). Clustering inference was based on the result obtained from Bayesian clustering model with ΔK values.

4.1.5. Genetic Variation among Clusters

The analysis of molecular variance (AMOVA) revealed the presence of higher genetic variance between populations inferred from structure analysis (52.41%) than among individuals within populations (47.59%) (**Table 6**). Further cluster analysis of AMOVA between the 25 varieties and 167 landrace accessions showed higher genetic variation between groups (61.02%) than individuals within the two groups (38.98%) (**Table 7**).

Table 6. Analysis of molecular variance (AMOVA) for Ethiopian durum wheat accessions with and without grouping according to clustering result based on SNPs data.

Source of variation	DF	Sum of squares	Variance components	Percentage of variation	Fixation indices	P value
Among populations	2	166172.20	700.94 Va	52.41	FST = 0.52	Va and FST = 0.000
Among individuals						
Within populations	189	240563.25	636.41 Vb	47.59	FIS = 1.00	Vb and FIS = 0.000
Total	191	406735.45	1337.35			

Table 7. Analysis of molecular variance (AMOVA) between landraces and varieties.

Source of variation	DF	Sum of squares	Variance components	Percentage of variation	Fixation indices	P value
Among populations	1	108435.72	1228.63 Va	61.02	FST = 0.61	Va and FST = 0.000
Among individuals						
Within populations	190	298299.73	784.99 Vb	38.98	FIS = 1.00	Vb and FIS = 0.000
Total	191	406735.45	2013.62			

4.1.6. Genetic Divergence between Landraces and Varieties

The Bayesian model based stratification and PCA clustering methods clearly grouped landraces and varieties in distinct places. The numbers of polymorphic SNPs were

slightly higher in varieties than landraces (**Table 4**). Varieties scored higher gene diversity (0.297), PIC (0.240) and the mean frequency of minor allele (0.218) than landraces (gene diversity = 0.213; PIC = 0.173 & MAF = 0.154).

4.1.7. Genetic Clustering Via Geographic Origin

The current panel comprises accessions from major wheat-producing areas of the country including Bale, Gondar, Gojjam, Shewa, Tigray, and Wollo, plus 12 landraces, which were originally from Ethiopia but currently cultivated in the USA.

Clustering analysis indicated that the SNPs data was unable to cluster landraces clearly based on their geographical backgrounds and accessions were admixed into the different sub-groups irrespective of their geographic origin. For instance, eight landraces collected from northeastern Ethiopia (Wollo) were grouped in sub-population one while 25 landraces from the same origin clustered in sub-population three (**Appendix Table 1**). Landraces collected from central Ethiopia (Shewa) clustered in both sub-group one (4 landraces) and three (19 landraces). However, from the total of eight landraces collected from Bichena (a town in East Gojjam Zone, west-central Ethiopia), seven of them were grouped in sub-population three and the other one landrace together with four landraces collected from other parts of Gojjam were grouped in sub-population one. Landraces collected from Bale (Southeastern Ethiopia) grouped in both clusters (44 landraces in cluster 1 and 24 landraces in cluster 3). The two landraces collected from Tigray region (North Ethiopia) were clustered in sub-population one. However, a landrace collected from Gondar (North Ethiopia) was sub-grouped in cluster three. All twelve Ethiopian landraces that are now cultivated in the USA were gathered in sub-population three.

4.2. Genome-Wide Association Analysis for Seminal Root System Architecture Traits

4.2.1. Phenotypic Variation among Root System Architecture (RSA) Traits

Analysis of variance (ANOVA) for the studied RSA traits is presented in **Table 8** and histogram for the distribution frequency in **Figure 13**. The distribution frequency shows more-or-less a normal distribution except for the trait, the presence of the 6th seminal root (RT6), that shows somehow a bi-modal type of distribution.

The ANOVA result indicates the presence of highly significant variation among accessions for all RSA traits. To add further details, the seminal root angle showed a wider divergence ranged from 45.7° to 130.5° with a mean value of 97.3°. The total and average root length and number of roots stretched from minimum values of 66.2, 16.5 and 3.4 cm to the maximum values of 195.4, 36.9 and 6.7 cm, respectively. The root and shoot weight was varied from the maximum values of 115.0 and 116.6 g to the minimum values of 27.7 and 34.7 g, respectively. The value of coefficient of variance (CV) of RSA traits ranged from 14.63 for root growth angle (RGA) to 8.38 for average root length (ARL). Individual root dry weight (IRW) and bulked root dry weight (RDW) also scored higher CV next to RGA with a value of 14.55 and 14.22%, respectively.

High level of broad-sense heritability (H^2) is scored for most RSA traits. Bulked root dry weight (RDW), average root length (ARL) and bulked shoot dry weight (SDW) took the top three with a score of 91.29, 91.03 and 90.36 %, respectively. The lowest heritability is scored by the presence of 6th root with a value of 67.04%.

4.2.2. Correlation among RSA traits and Varieties vs Landraces Mean

Performance

A strong correlation was observed between RSA traits (**Figure 4.5**). A highly significant positive correlation was observed between root dry weight and individual roots dry weight; root dry weight & shoot dry weight and individual root dry weight and shoot dry weight with a correlation coefficient of 0.93, 0.92 and 0.84, respectively. The other and expected strong correlations were recorded between total root number and the presence of the 6th root, root length and average root length with a correlation coefficient of 0.84 and 0.82, respectively. The initial thousand grain weight (iTGW) showed no significant correlation with any RSA trait signifying that variation of RSA traits did not have maternal etiology.

The varieties mean value for root and shoot dry weight traits were 90.3 and 92.8 g, respectively while landraces could only score 56.89 and 66.49 g for the same trait, respectively. Varieties also performed better than landraces in traits including TRL and ARL. Total root number (TRN) was the only trait that landraces scored slightly higher than varieties. Varieties were slightly higher than landraces for the mean value of iTGW.

Table 8. ANOVA and heritability results for the root system architecture (RSA) traits measured at 12-day-old seedlings for Ethiopian durum wheat accessions.

	TRL ^a (cm)	ARL (cm)	RGA (°)	TRN (n)	RDW (mg)	IRW (mg)	SDW (mg)	RSR (ratio)	RT6 (%)
Mean	135.3	26.1	97.3	5.1	60.5	11.6	69.5	0.87	37.2
Max	195.4	36.9	130.5	6.7	115.0	21.4	116.6	1.32	100
Min	66.2	16.5	45.7	3.4	27.7	5.9	34.7	0.67	0
H² (%)	88.97	91.03	74.26	75.07	91.29	89.91	90.36	71.25	67.04
CV (%)	11.09	8.38	14.63	8.09	14.22	14.55	11.49	10.49	— ^b
P accessions^c	***	***	***	***	***	***	***	***	***
P replicates^d	NS	NS	NS	*	*	*	NS	*	*

^a RSA trait acronyms: TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight/experiment; IRW, individual root dry weight; SDW, shoot dry weight/experiment; RSR, root to shoot ratio; RT6, presence of the sixth root

^b Not reported due to the presence of many values equal to 0.00

^c Significance of the difference between accessions

^d Significance of the difference between replicates.

NS = non-significant; * P < 0.05; ** P < 0.01; ***P < 0.001

Table 9. Mean values of varieties and landraces for RSA traits.

Accession type	iTGW (mg)	TRL (cm)	ARL (cm)	RGA (°)	TRN (n)	RDW (mg)	SDW (mg)	RSR (ratio)	RT6 (%)
Variety	45.90	161.50	31.84	99.79	5.09	90.29	92.81	0.97	0.30
Landrace	42.28	132.01	25.40	98.06	5.20	56.89	66.49	0.86	0.38

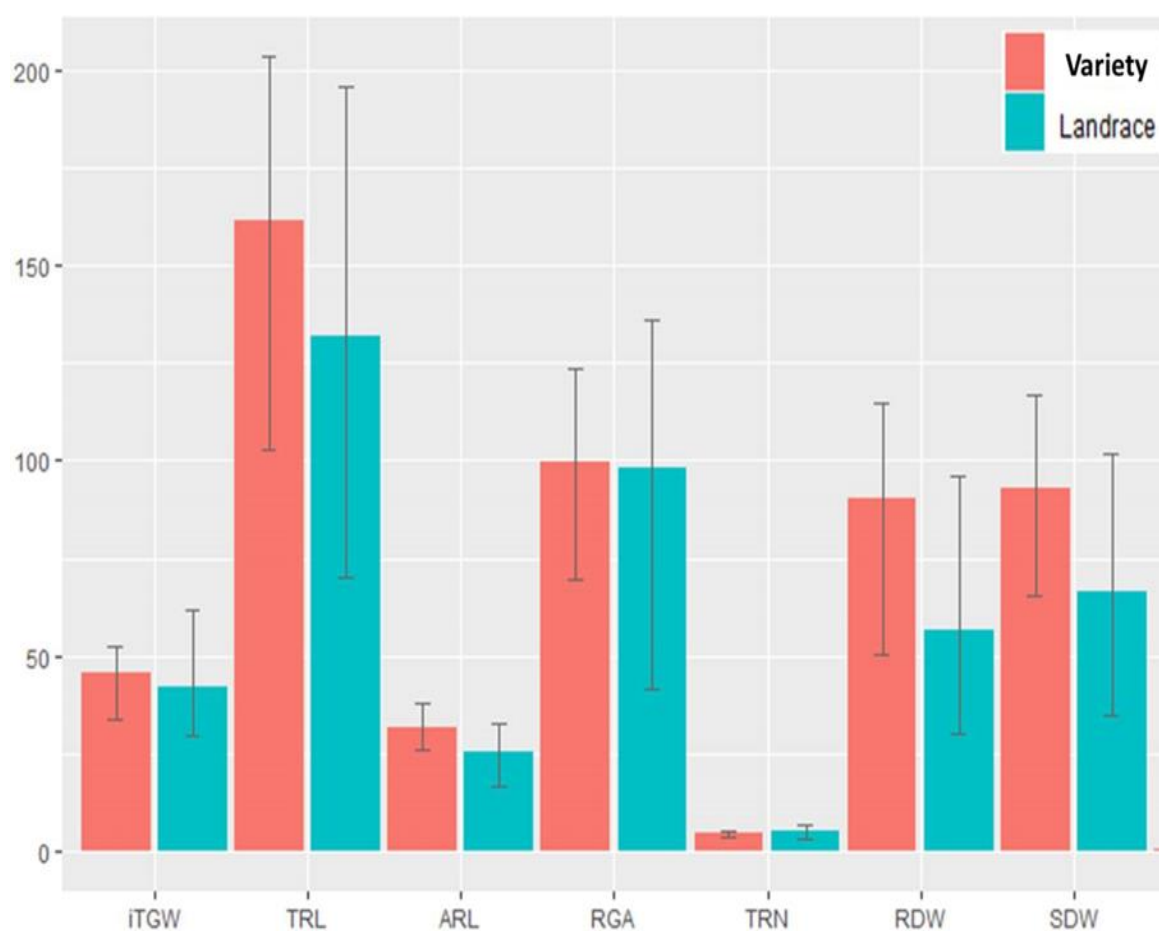


Figure 13. Bar chart of Ethiopian durum wheat varieties and landraces for means of RSA traits. RSA trait acronyms: iTGW, initial thousand grain weight; TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight; SDW, shoot dry weight

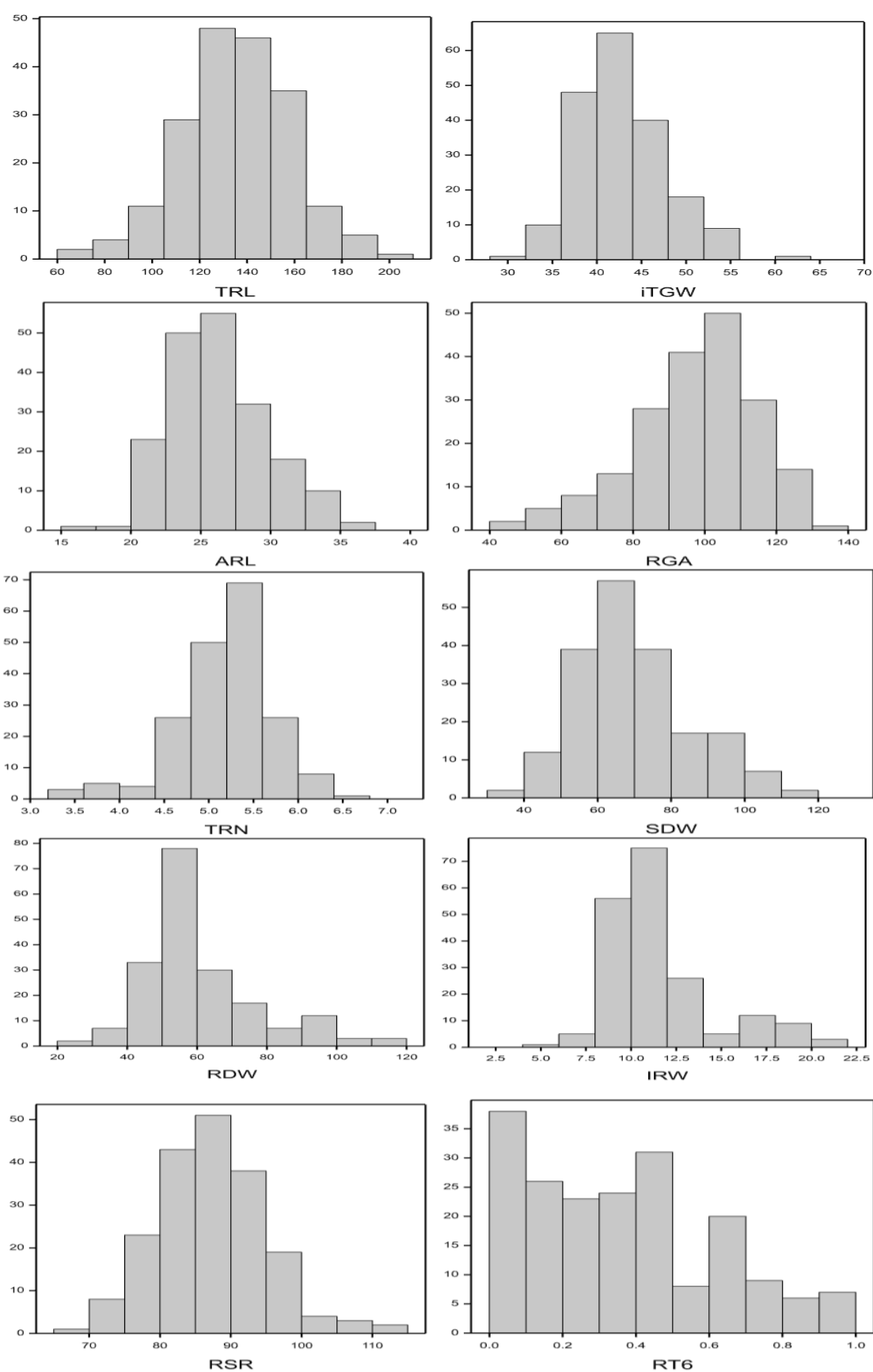


Figure 14. Distribution frequency for root system architecture (RSA) traits measured in 12-day-old seedlings in Ethiopian durum wheat accessions.



Figure 15. Correlation coefficient and level of significance for the initial thousand-grain weight and RSA traits measured at the 12-day-old seedlings for Ethiopian durum wheat accessions. RSA trait acronyms: iTGW, initial thousand grain weight; TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight; SDW, ; IRW, individual root dry weight ; shoot dry weight; RSR, root to shoot ratio; Rt6, presence of the sixth root

Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

4.2.3. GWAS Analysis of RSA Traits

A total of 277 QTLs with various significant values were identified for all tested RSA traits. The only four major QTLs which were able to exceed the experiment-wise threshold ($-\log P \geq 4$) were *EPdwRGA-6A*, *EPdwRDW-4A*, *EPdwiTGW-3B.1* and *EPdwIRW-5A* with 6.85, 4.34, 4.15 and 4.06 scoring a phenotypic variation (r^2) of 16.08, 8.41, 8.71 and 8.03 %, respectively. A total of thirty-four QTLs were able to reach the marker-wise threshold of $-\log P \geq 3$ in which the highest number was

identified for TRN with 8 QTLs followed by SDW and IRW scored 6 QTLs for each traits. Three equal number of nominal QTLs were able to identify for TRL, iTGW, and RT6; 2 nominal QTLs for RDW and only one QTLs for each of the rest (RGA, ARL and RSR) traits. The other 239 QTLs were identified as a suggestive QTLs with a marker-wise threshold of $-\log P \geq 2$. The major and nominal QTLs are reported in **Table 10** while the whole list of identified QTLs with the marker-wise threshold value of $-\log P \geq 2$ are stated in **Appendix Table 4**. Thirteen markers have shown significant associations for more than one RSA trait that could be a pleiotropic effect/tightly linked and treated as separate QTLs for corresponding traits (**Table 11**). It is noteworthy that root growth angle showed a clear distinction from other RSA traits.

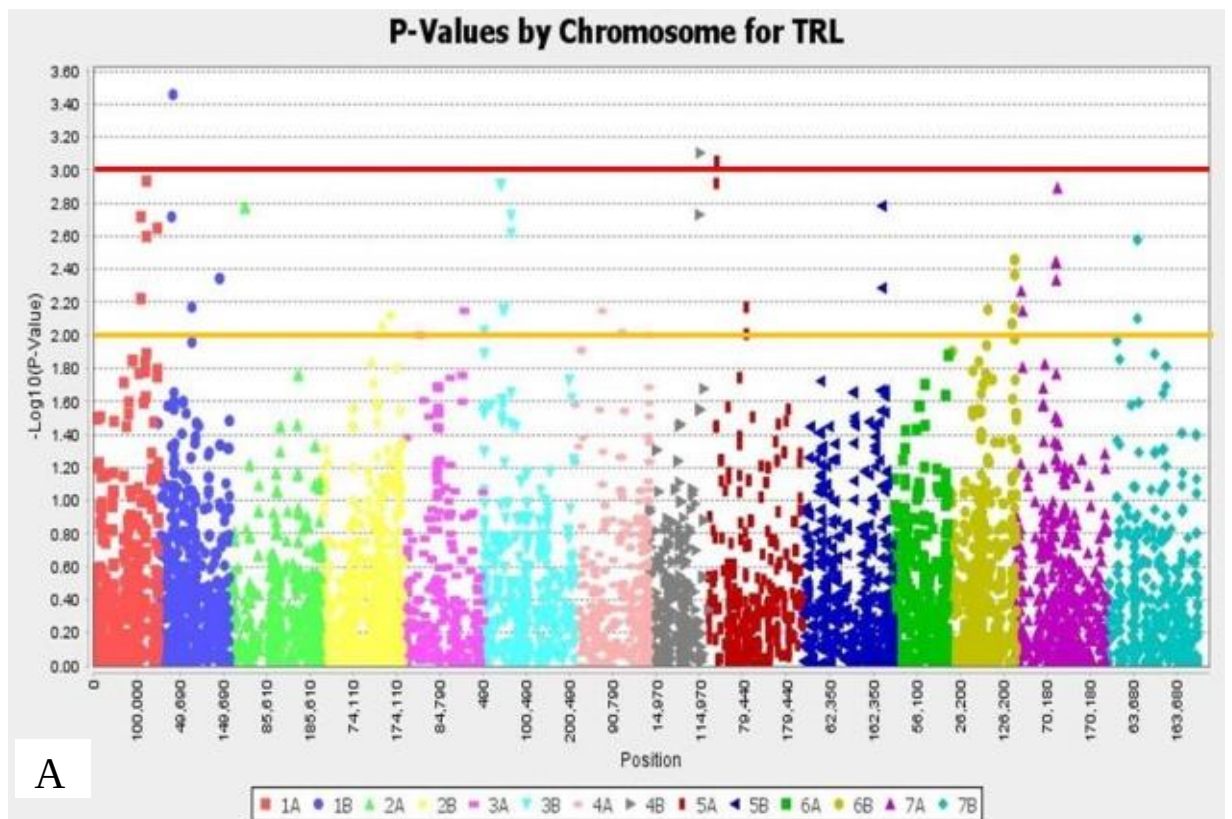
4.2.4. QTL Clusters for RSA Traits

Identified QTLs were further grouped into 15 RSA QTL clusters plus one special RGA QTLs cluster (on the long arm of chromosome 6A) across chromosomes based on the significance of single QTL and effect on various QTLs in this particular study and overlapping with previously reported studies in both bread and durum wheat (**Table 14**). From the total identified QTLs, 103 were able to included in the 16 QTL clusters. Two clusters from chromosomes 1A, 3B and 7A and one cluster from chromosomes 1B, 2A, 2B, 3A, 4A, 4B, 5A, 5B, 6A, and 6B were appeared (**Figure 28; 29**).

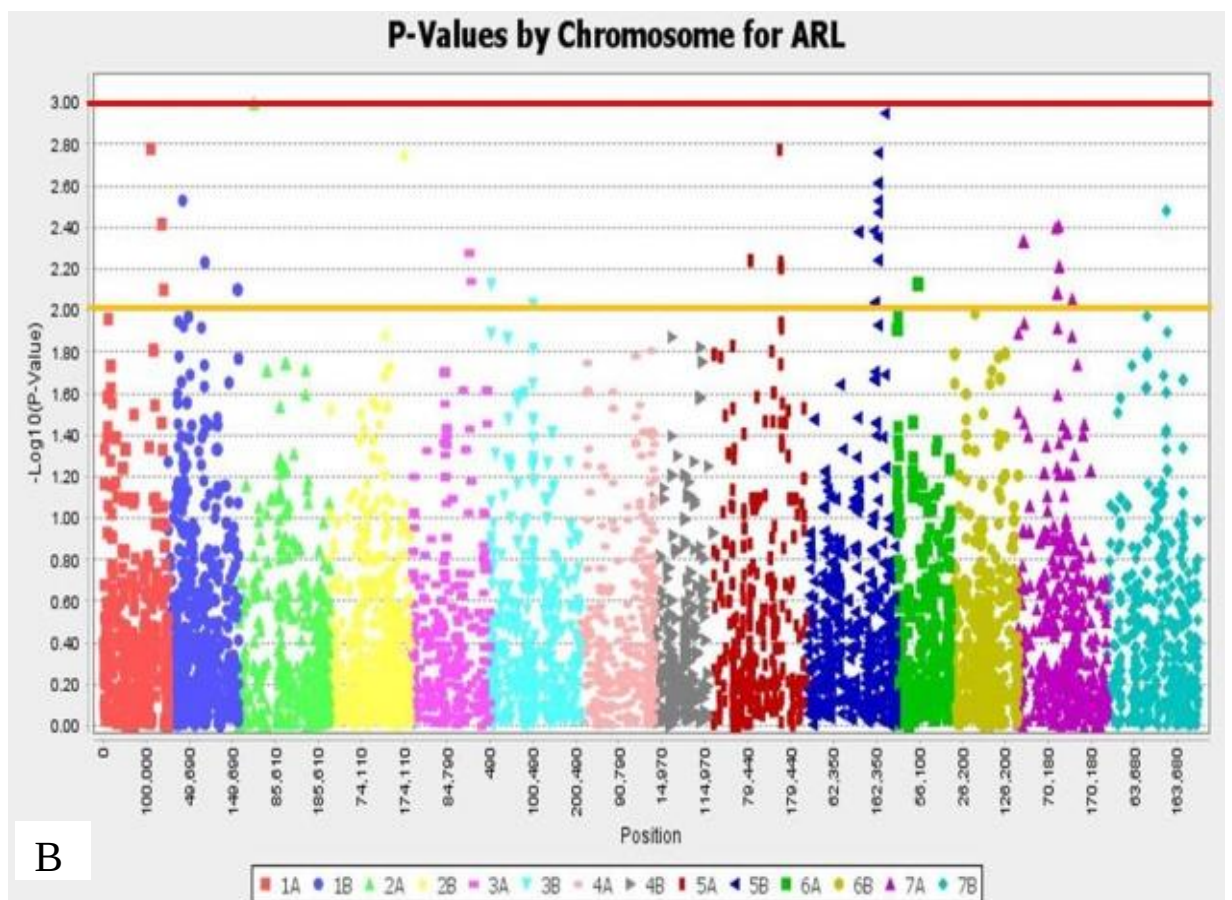
4.2.5. QTLs for Seminal Root Length and Number

EPdwTRL-1B at RSA QTL-cluster-3, *EPdwTRL-4B* at RSA QTL-cluster-10 and *EPdwTRL-5A* at RSA QTL-cluster-11 were the three nominal QTLs identified for

total root length on chromosomes 1B, 4B and 5A, respectively (**Figure 16**). Other suggestive TRL QTLs identified across all chromosomes except on chromosome 6A. Only one nominal QTL, *EPdwARL-2A* at RSA QTL-cluster-4, was spotted for average root length on chromosome 2A. However, other ARL suggestive QTLs were identified in all chromosomes. Seven nominal QTLs detected for total root number: three QTLs (*EPdwTRN-4B.1*, *EPdwTRN-4B.2* and *EPdwTRN-4B.3*) on chromosome 4B of which the later two appeared at RSA QTL-cluster-10; two QTLs (*EPdwTRN-1A.1* and *EPdwTRN-1A.2*) on chromosome 1A at RSA QTL-cluster-1; *EPdwTRN-1B* at RSA QTL-cluster-2, *EPdwTRN-4A* at RSA QTL-cluster-9 and *EPdwTRN-7A* at RSA QTL-cluster-15 on chromosomes 1B, 4A and 7A, respectively. Suggestive QTLs were also identified for TRN across all chromosomes except on chromosomes 2A and 5A. For the presence of the sixth seminal root, three QTLs (*EPdwRT6-4B.1*, *EPdwRT6-4B.2*, *EPdwRT6-4B.3* of which the later two appeared at RSA QTL-cluster-10) were spotted on chromosome 4B (**Table 10**). The allelic distribution and frequency of RGA, TRN and IRW QTL-tagging SNPs with phenotypic effect > 5% is reported in **Appendix Table 5, 6 and 7**, respectively.



A



B

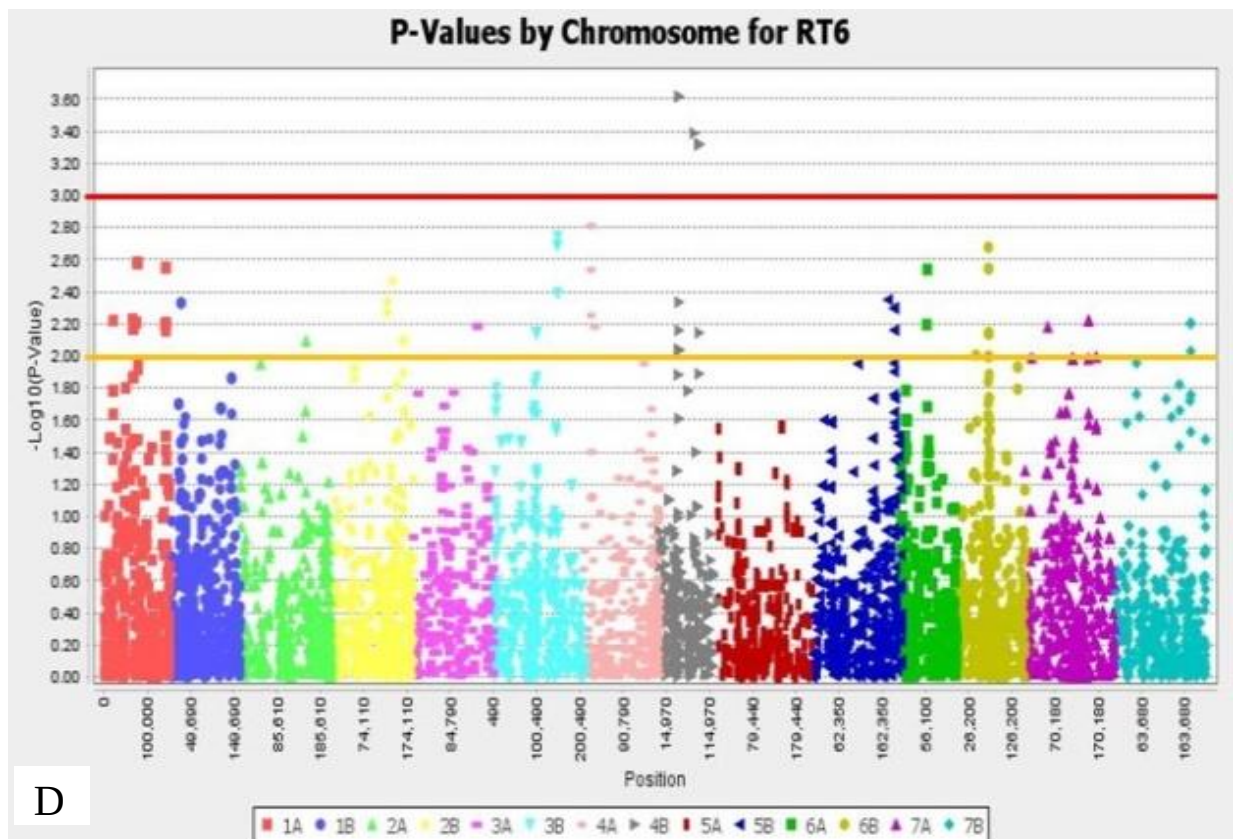
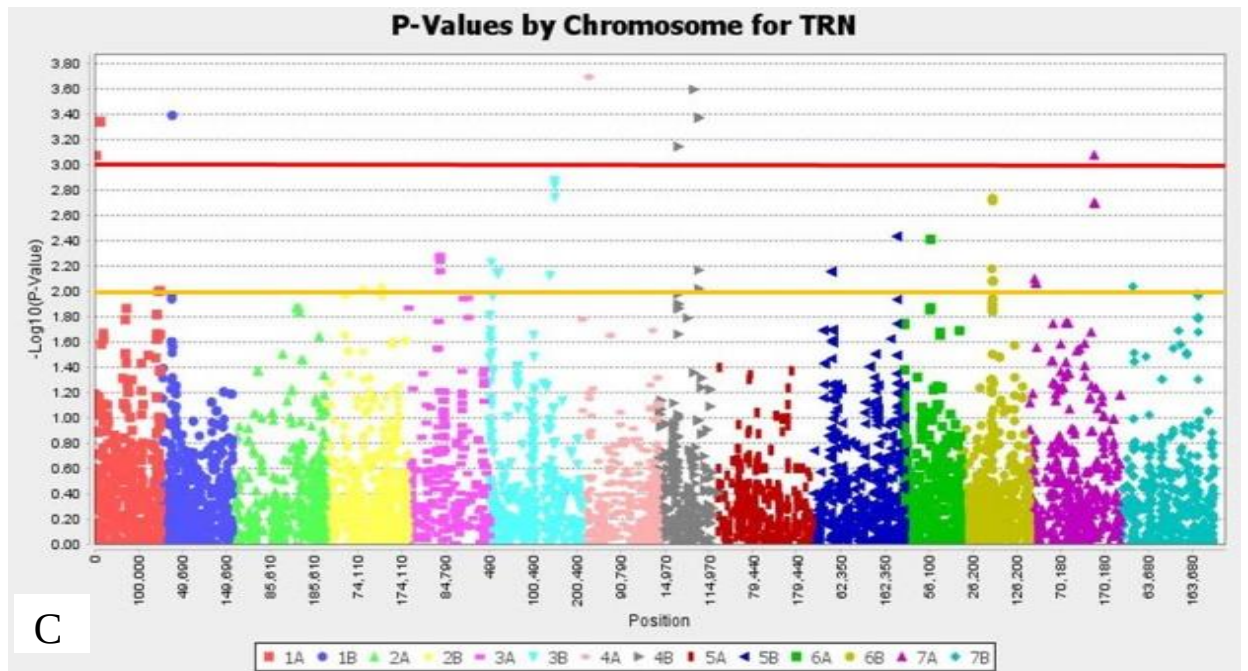


Figure 16. Manhattan plot for P-values of associations with total root length (A), average root length (B), total root number (C) and presence of more than 6 roots (D) across chromosomes in 192 Ethiopian durum wheat accessions. The orange and red horizontal lines designate the significant association thresholds for suggestive ($-\log_{10} P \geq 2$) and nominal ($-\log_{10} P \geq 3$) QTLs, respectively.

4.2.6. QTLs for Seminal Root Growth Angle

A major QTL (*EPdwRGA-6A*) was identified on chromosome 6A that explained 16.1% of the total phenotypic variance. Along with this, six different markers (*IWB35245*, *IWB71122*, *IWB24306*, *IWB57413*, *IWB10077* and *IWB74235*) within the confidence interval, have shown a strong associations for this QTL (**Appendix Table 4, Figure 17**). A unique RGA QTLs cluster was identified on chromosome 6A in between 105-125 cM that included five RGA-QTLs (**Figure 28**). In addition, *EPdwRGA-4A* was the other nominal QTL identified on chromosome 4A. Other RGA suggestive QTLs were identified on chromosomes 1A, 2B, 3A, 3B, 5B, 6B, 7A and 7B (**Appendix Table 4**). Notably, RGA QTLs showed no clustering with the other RSA trait QTLs.

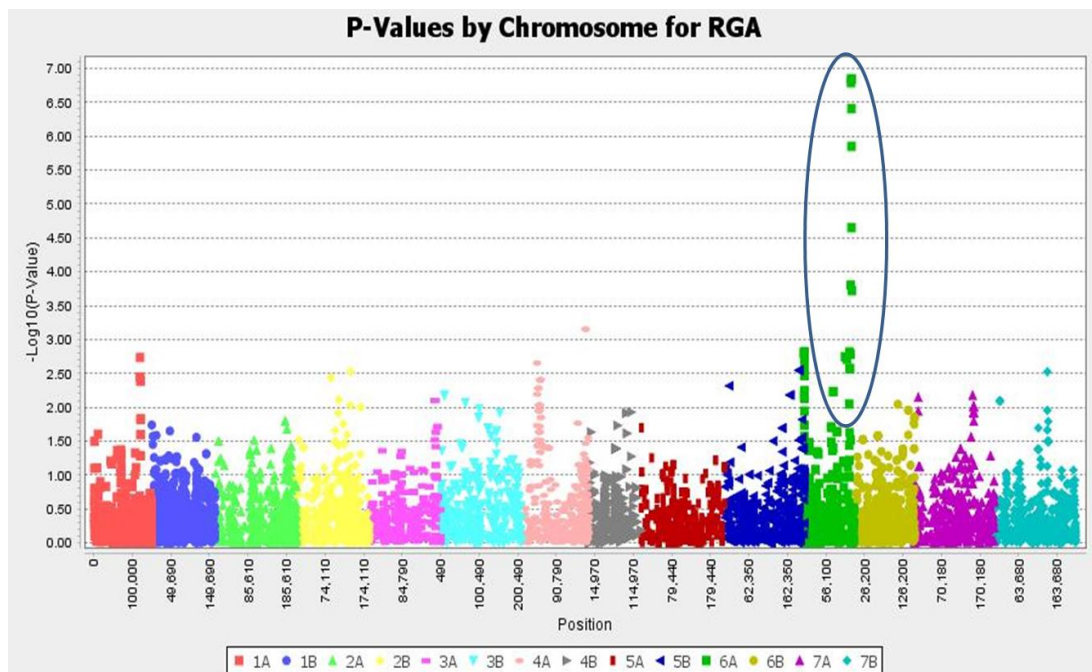
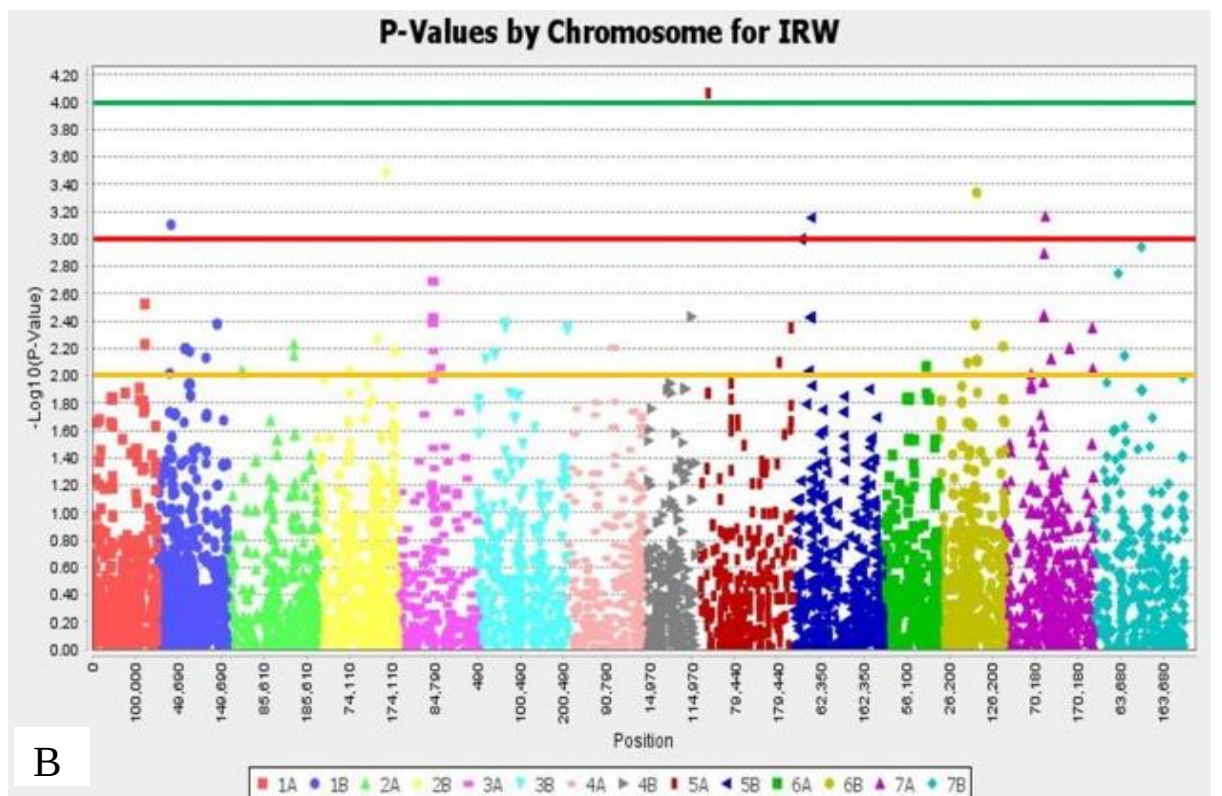
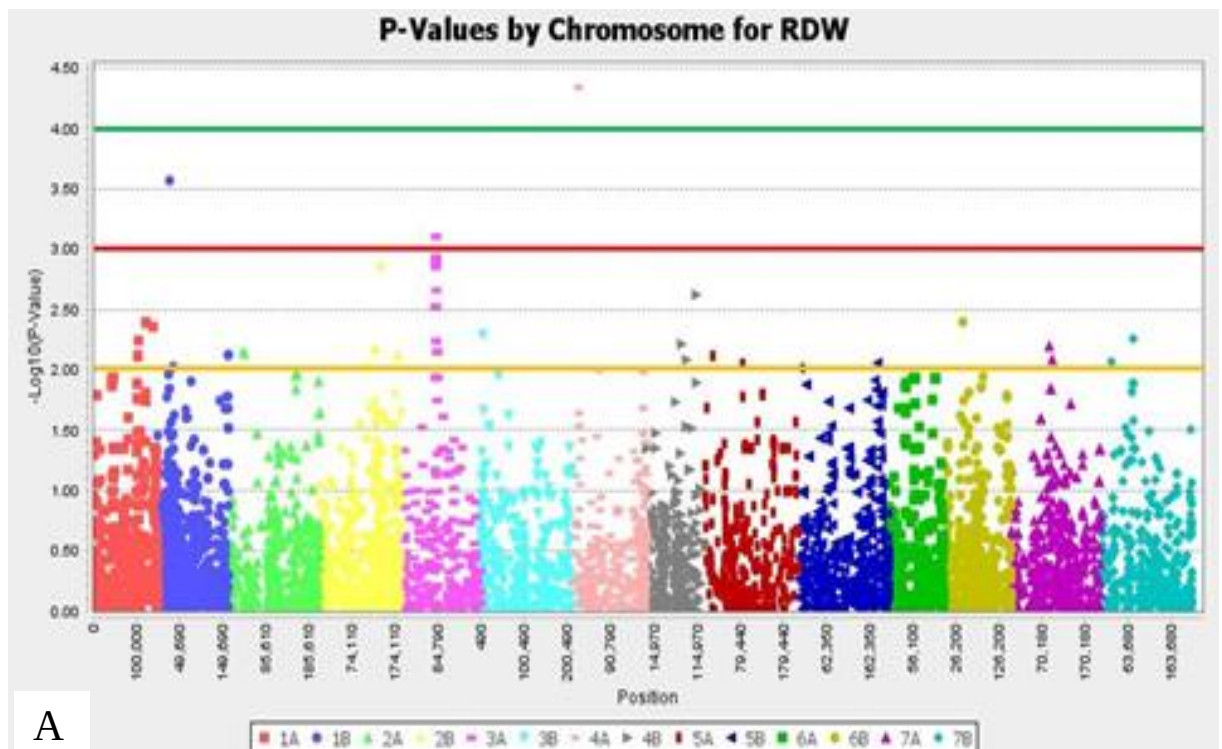


Figure 17. Manhattan plot for root growth angle (RGA) that showed a strong QTL on chromosome 6A.

4.2.7. QTLs for Root and Shoot Dry Weight

EPdwRDW-4A (at RSA QTL-cluster-9) and *EPdwIRW-5A* (at RSA QTL-cluster-11) are the two major QTLs identified for bulked root dry weight and individual root dry weight on chromosomes 4A and 5A, respectively (**Figure 18**). Two nominal QTLs for RDW (*EPdwRDW-1B* at RSA QTL-cluster-3 and *EPdwRDW-3A* at RSA QTL-cluster-6) and six for IRW (*EPdwIRW-1B* at RSA QTL-cluster-3, *EPdwIRW-2B* at RSA QTL-cluster-5; *EPdwIRW-5B.1* and *EPdwIRW-5B.2* at RSA QTL-cluster-12, *EPdwIRW-6B* at RSA QTL-cluster-13 and *EPdwIRW-7A* at RSA QTL-cluster-14) were spotted. Five nominal QTLs (*EPdwSDW-1A* at RSA QTL-cluster-2, *EPdwSDW-1B* at RSA QTL-cluster-3, *EPdwSDW-3B* at RSA QTL-cluster-6, *EPdwSDW-4A* at RSA QTL-cluster-9, *EPdwSDW-4B* at RSA QTL-cluster-10 and *EPdwSDW-5B*) were identified for bulked shoot weight. RDW, IRW and SDW have repetitively clustered at nearby or in single QTL (**Table 14**).



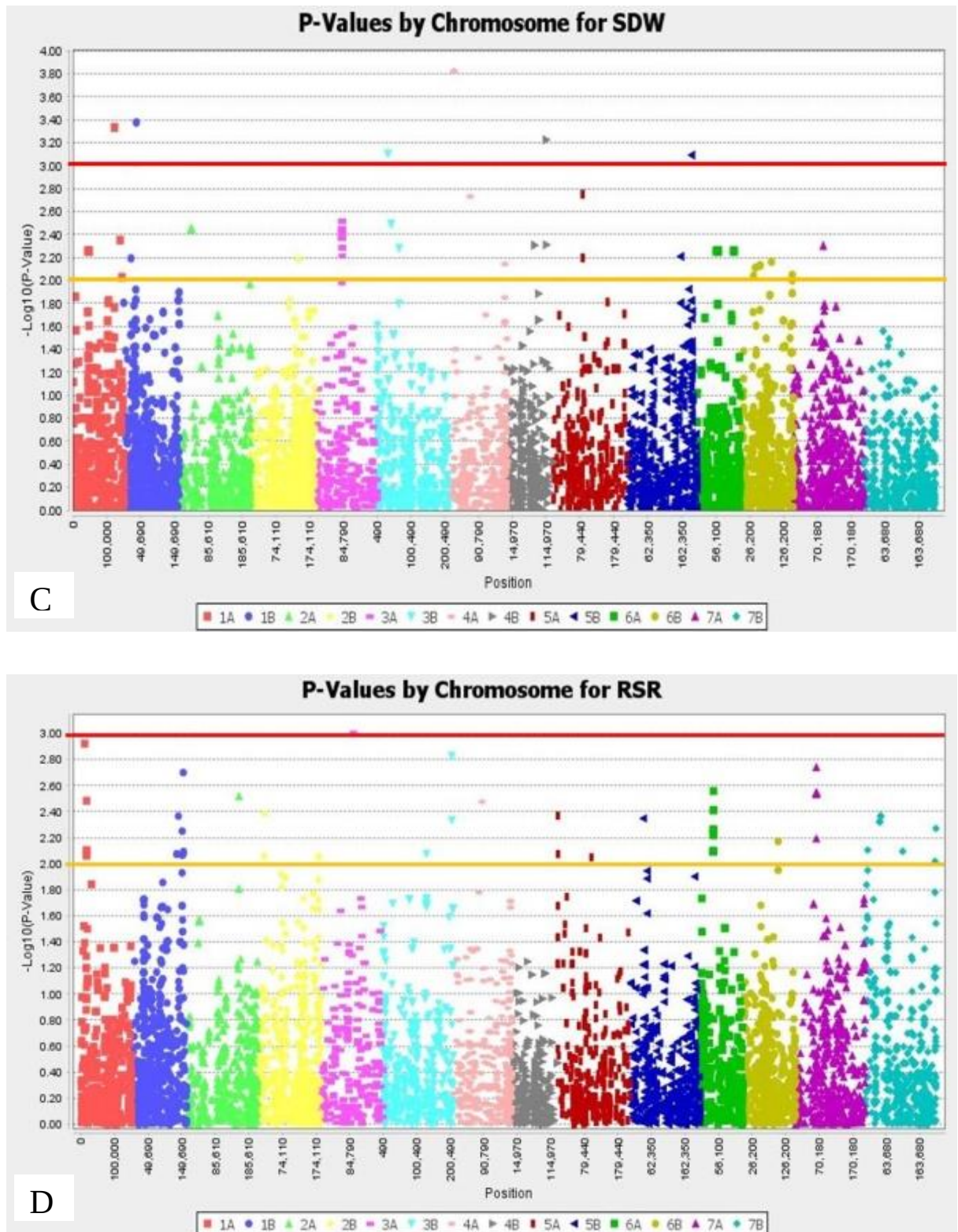


Figure 18. Manhattan plot for P-values of MTA with root dry weight (A), individual root weight (B), shoot dry weight (C) and root shoot ratio (D) across chromosomes in 192 Ethiopian durum wheat accessions. The orange, red and green horizontal lines designates the significant association thresholds for suggestive ($-\log_{10} P \geq 2$), nominal ($-\log_{10} P \geq 3$) and major ($-\log_{10} P \geq 4$) QTLs, respectively.

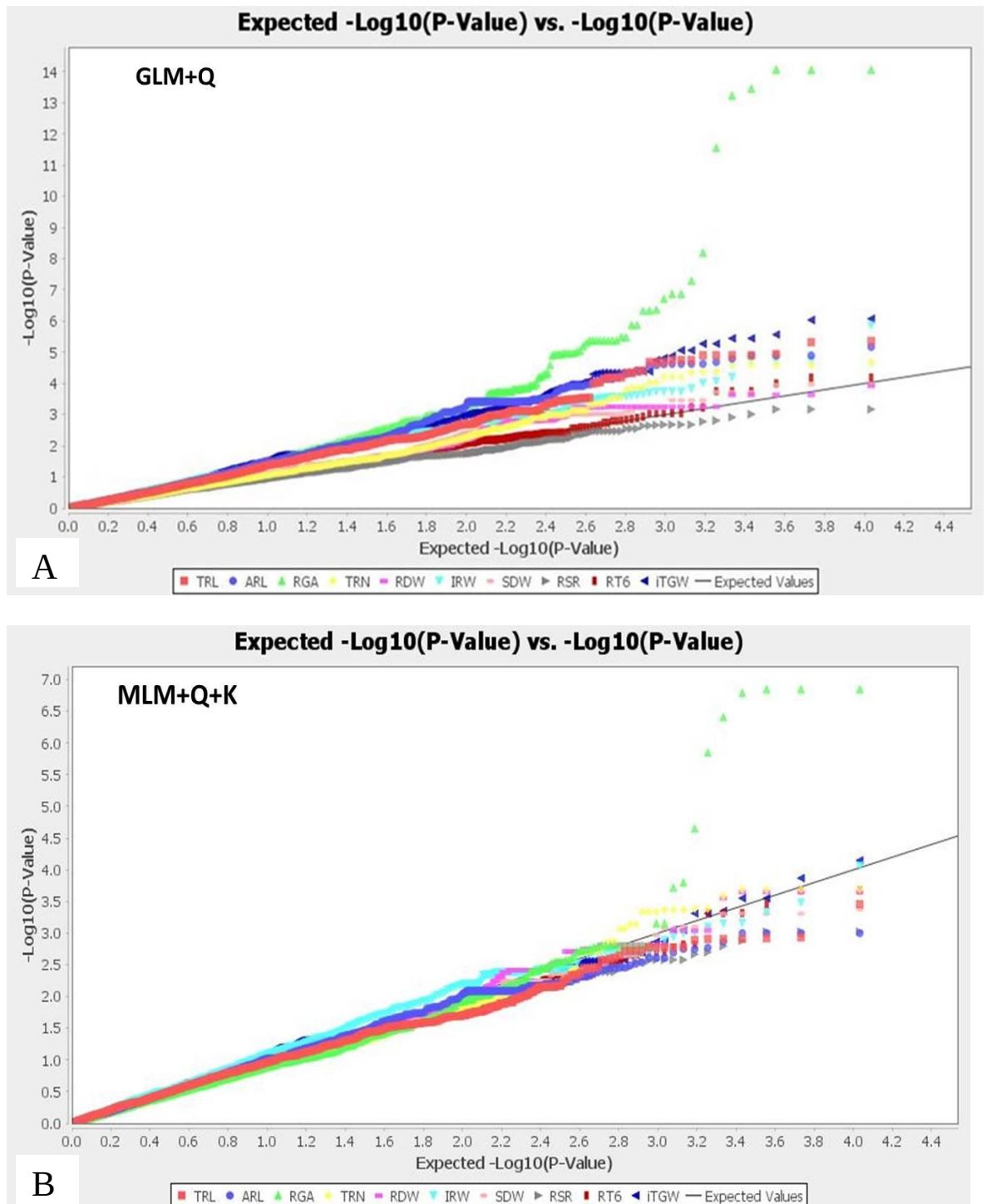


Figure 19. Q-Q (quantile-quantile) plot results of the GWAS analysis for RSA traits using different methods: General Linear Model with population structure (GLM+Q)(A); Mixed Linear Model with population structure and kinship matrix (MLM+Q+K) (B). Acronyms: iTGW, initial thousand grain weight; TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight; SDW, shoot dry weight ; IRW, individual root dry weight ; RSR, root to shoot ratio; RT6, presence of the sixth root.

Table 10. List of identified major and nominal QTLs for root system architecture (RSA) traits in Ethiopian durum wheat.

QTL	Trait ^a	Marker ^b	Chr	Position (cM)	P-value	P (-log10)	R ² (%)	Sig. SNPs ^c	CI (cM) ^d	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
<i>EPdwTRL-1B</i>	TRL	<i>IWB60732</i>	1B	33.75	0.000349	3.46	6.75	0	31.5-36	A	16.08	41	G	0	151
<i>EPdwTRL-4B</i>	TRL	<i>IWB23476</i>	4B	114.43	0.000761	3.12	5.67	0	112.18-116.68	A	8.8	154	G	0	38
<i>EPdwTRL-5A</i>	TRL	<i>IWA3196</i>	5A	16.83	0.000845	3.07	5.57	1	14.58-19.08	C	39.84	126	T	0	66
<i>EPdwARL-2A</i>	ARL	<i>IWB53380</i>	2A	35.63	0.001	3.00	5.72	3	33.38-37.88	A	4.76	159	G	0	33
<i>EPdwRGA-6A</i>	RGA	<i>IWB71119</i>	6A	122.43	1.42E-07	6.85	16.08	8	120.18-124.68	C	-22.31	113	T	0	79
<i>EPdwRGA-4A</i>	RGA	<i>IWB69385</i>	4A	167.15	0.000703	3.15	6.38	1	164.9-169.94	G	13.44	78	T	0	114
<i>EPdwTRN-1A.1</i>	TRN	<i>IWB8696</i>	1A	5.20	0.00085	3.07	5.71	0	2.95-7.45	A	0.78	31	G	0	161
<i>EPdwTRN-1A.2</i>	TRN	<i>IWB12589</i>	1A	13.62	0.00046	3.34	6.32	2	11.37-15.87	A	0.57	16	G	0	176
<i>EPdwTRN-1B</i>	TRN	<i>IWB35568</i>	1B	27.21	0.00041	3.39	6.43	1	24.96-29.46	A	0.54	111	G	0	81
<i>EPdwTRN-4A</i>	TRN	<i>IWB21309</i>	4A	17.01	0.000204	3.69	7.13	3	14.76-19.26	C	-0.43	87	T	0	105
<i>EPdwTRN-4B.1</i>	TRN	<i>IWB10265</i>	4B	44.92	0.000724	3.14	5.87	1	42.67-47.17	A	0.39	138	G	0	54
<i>EPdwTRN-4B.2</i>	TRN	<i>IWB35047</i>	4B	80.4	0.000256	3.59	6.90	0	78.15-82.65	C	-0.44	91	G	0	101
<i>EPdwTRN-4B.3</i>	TRN	<i>IWB66095</i>	4B	91.74	0.000429	3.37	6.39	4	89.49-93.99	C	0.52	47	T	0	145
<i>EPdwTRN-7A</i>	TRN	<i>IWB3767</i>	7A	146.9	0.000844	3.07	5.72	3	144.65-149.15	C	0.5	171	T	0	21
<i>EPdwRDW-1B</i>	RDW	<i>IWB60732</i>	1B	33.75	0.00028	3.55	6.72	1	31.5-36	A	10.59	41	G	0	151
<i>EPdwRDW-3A</i>	RDW	<i>IWB67049</i>	3A	80.8	0.000682	3.17	5.76	54	78.55-83.05	A	-14.1	15	G	0	177
<i>EPdwRDW-4A</i>	RDW	<i>IWB21309</i>	4A	17.01	4.59E-05	4.34	8.41	3	14.76-19.26	C	-9.81	87	T	0	105
<i>EPdwSDW-1A</i>	SDW	<i>IWB29244</i>	1A	123.21	0.000465	3.33	6.27	2	120.96-125.46	C	-9.18	138	T	0	54

Table 10. *Continued*

QTL	Trait ^a	Marker ^b	Chr	Position (cM)	P-value	P(-log10)	R ² (%)	Sig. SNPs ^c	CI (cM) ^d	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
<i>EPdwSDW-1B</i>	SDW	<i>IWB60732</i>	1B	33.75	0.000419	3.38	6.58	0	31.5-36	A	13.4	41	G	0	151
<i>EPdwSDW-3B</i>	SDW	<i>IWB35437</i>	3B	41.34	0.000796	3.10	5.93	2	39.09-43.59	C	-17.57	36	T	0	156
<i>EPdwSDW-4A</i>	SDW	<i>IWB21309</i>	4A	17.01	0.000151	3.82	7.39	3	14.76-19.26	C	-8.2	87	T	0	105
<i>EPdwSDW-4B</i>	SDW	<i>IWB23476</i>	4B	114.43	0.000594	3.23	6.03	1	112.18-116.68	A	15.41	154	C	0	38
<i>EPdwSDW-5B</i>	SDW	<i>IWB8808</i>	5B	190.51	0.000809	3.09	5.73	0	188.26-192.76	A	-9.41	36	C	0	156
<i>EPdwiTGW-3B.1</i>	iTGW	<i>IWB65507</i>	3B	126.23	7.09E-05	4.15	8.71	2	123.98-128.48	A	-9.84	160	G	0	32
<i>EPdwiTGW-3B.2</i>	iTGW	<i>IWB11298</i>	3B	129.61	0.000135	3.87	8.01	12	127.36-131.86	A	10.94	160	C	0	32
<i>EPdwiTGW-7A</i>	iTGW	<i>IWB7752</i>	7A	98.3	0.000448	3.35	6.73	1	96.05-100.55	A	-7.27	173	G	0	19
<i>EPdwiTGW-7B</i>	iTGW	<i>IWB60</i>	7B	33.71	0.000486	3.31	6.64	1	31.46-35.96	A	3.83	28	C	0	164
<i>EPdwIRW-1B</i>	IRW	<i>IWB60732</i>	1B	33.75	0.000789	3.10	5.80	0	31.5-36	A	1.7	41	G	0	151
<i>EPdwIRW-2B</i>	IRW	<i>IWB29332</i>	2B	160.51	0.000328	3.48	6.68	0	158.26-162.76	A	4.5	24	G	0	168
<i>EPdwIRW-5A</i>	IRW	<i>IWA3196</i>	5A	16.83	8.64E-05	4.06	8.03	0	14.58-19.08	C	7.54	26	T	0	166
<i>EPdwIRW-5B.1</i>	IRW	<i>IWB70122</i>	5B	40.39	0.000702	3.15	5.92	7	38.14-12.64	A	2.81	16	C	0	176
<i>EPdwIRW-5B.2</i>	IRW	<i>IWA332</i>	5B	16.73	0.00101	3	5.56	1	14.48-18.89	G	-2.96	15	T	0	177
<i>EPdwIRW-6B</i>	IRW	<i>IWB73456</i>	6B	90.33	0.00046	3.34	6.34	4	88.08-92.58	C	2.94	21	T	0	171
<i>EPdwIRW-7A</i>	IRW	<i>IWB11841</i>	7A	94.72	0.000684	3.17	5.94	0	92.47-96.97	C	-1.43	66	T	0	126
<i>EPdwRSR-3A</i>	RSR	<i>IWB25948</i>	3A	96.93	0.000947	3.02	4.62	2	94.68-99.18	C	-0.1	170	T	0	22
<i>EPdwRT6-4B.1</i>	RT6	<i>IWB72884</i>	4B	45.01	0.000211	3.68	7.13	7	42.76-47.26	A	0.21	138	G	0	54
<i>EPdwRT6-4B.2</i>	RT6	<i>IWB35047</i>	4B	80.4	0.000351	3.45	6.62	0	78.15-82.65	C	-0.22	91	G	0	101
<i>EPdwRT6-4B.3</i>	RT6	<i>IWB66095</i>	4B	91.74	0.000481	3.32	6.30	3	89.49-93.99	C	0.28	47	T	0	145

^a RSA trait acronyms: iTGW, initial thousand grain weight; TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight/experiment; IRW, individual root dry weight; SDW, shoot dry weight/experiment; RSR, root to shoot ratio; Rt6, presence of the sixth root.

^b A SNP found at the peak of corresponding QTL (QTL-tag SNP).

^c The number of significant SNPs existed in the significant interval.

^d Confident interval from the left and right of QTL-tag SNP based on the tetraploid wheat consensus map (Maccaferri *et al.*, 2015)

Table 11. List of markers with a significant association/pleiotropic effect with more than one RSA trait.

Marker*	QTL	Chr	Position (cM)	Traits**	P(-log10)	R ² (%)	CI (cM)
<i>IWB29244</i>	<i>EPdwSDW-1A</i>	1A	123.21	SDW	3.3	6.3	120.96 - 125.46
				RDW	2.3	3.9	
<i>IWB60732</i>	<i>EPdwRDW-1B</i>	1B	33.75	RDW	3.6	6.7	31.5 - 36
	<i>EPdwSDW-1B</i>			SDW	3.4	6.6	
	<i>EPdwTRL-1B</i>			TRL	3.5	6.8	
	<i>EPdwIRW-1B</i>			IRW	3.1	5.8	
<i>IWB35568</i>	<i>EPdwTRN-1B</i>	1B	27.21	TRN	3.4	6.4	24.96 - 29.46
				RT6	2.2	3.8	
<i>IWB53380</i>	<i>EPdwARL-2A</i>	2A	35.63	ARL	3.0	5.7	33.38 - 37.88
				IRW	2.0	3.4	
				RDW	2.4	4.1	
				SDW	2.6	4.9	
				TRL	2.8	5.2	
<i>IWB29332</i>	<i>EPdwIRW-2B</i>	2B	160.51	IRW	3.5	6.7	158.26 - 162.76
				TRL	2.1	2.12	
<i>IWB67049</i>	<i>EPdwRDW-3A</i>	3A	80.8	RDW	3.2	5.8	78.55 - 83.05
				SDW	2.4	4.3	
<i>IWB35437</i>	<i>EPdwSDW-3B</i>	3B	41.34	SDW	3.1	5.9	39.09 - 43.59
				RDW	2.6	4.9	
				IRW	2.2	3.7	

Table 11. Continued

Marker*	QTL	Chr	Position (cM)	Traits**	P(-log10)	r ² (%)	CI (cM)
<i>IWB21309</i>	<i>EPdwRDW-4A</i>	4A	17.01	RDW	4.3	8.4	14.76 - 19.26
	<i>EPdwSDW-4A</i>			SDW	3.8	7.4	
	<i>EPdwTRN-4A</i>			TRN	3.7	7.1	
				RT6	2.7	4.9	
<i>IWB35047</i>	<i>EPdwTRN-4B.2</i>	4B	80.41	TRN	3.6	6.9	78.15 - 82.65
	<i>EPdwRT6-4B.2</i>			RT6	3.5	6.6	
				SDW	2.3	4.0	
				RDW	2.1	3.5	
<i>IWB66095</i>	<i>EPdwTRN-4B.3</i>	4B	91.74	TRN	3.4	6.4	89.49 - 93.99
	<i>EPdwRT6-4B.3</i>			RT6	3.3	6.3	
<i>IWB23476</i>	<i>EPdwSDW-4B</i>	4B	114.43	SDW	3.2	6.0	112.18 - 116.68
	<i>EPdwTRL-4B</i>			TRL	3.1	5.7	
				IRW	2.4	4.3	
				RDW	2.2	3.7	
<i>IWA3196</i>	<i>EPdwIRW-5A</i>	5A	16.83	IRW	4.1	8.0	14.58 - 19.08
<i>IWB11841</i>	<i>EPdwIRW-7A</i>	7A	94.72	IRW	3.2	5.9	92.47 - 96.97
				TRL	2.9	5.4	
				RDW	2.4	4.1	
	<i>EPdwTRL-5A</i>			TRL	3.1	5.6	
				RDW	2.1	3.4	

* The common SNP found at the peak of corresponding QTLs (QTL-tag SNP) for group of RSA traits.

**Cluster of RSA traits that have shown a significant association with QTL-tag SNP

4.3. Genome-Wide Association Mapping for Grain Shape and Color Related Traits

4.3.1. Phenotypic Variation

A significant variation was observed between the means of accessions for all considered traits (**Table 12**). A maximum score of 8.7 and 3.6 mm and minimum value of 6.0 and 2.4 mm were scored for grain length and width with mean values of 7.5 mm and 3.0 mm, respectively. CIE L* (brightness) scored a mean value of 57.3 ranging from 43.5 to 67.9; CIE a* varied from 6.5 to 13.2 scoring a mean value of 9.6; and CIE b* scored a mean value of 16.1, ranging from 11.1 to 20.89. L* showed significant negative correlation with a* ($r = -0.97$, $P < 0.001$) and significant positive correlation with b* ($r = 0.79$, $P < 0.001$) (**Figure 20**). CIE a* had a significant negative correlation with GW ($r = -0.88$, $P < 0.001$), b* ($r = 0.80$, $P < 0.001$) and GL ($r = -0.62$, $P < 0.05$). Thousand grain weight didn't show any significant correlation with neither grain shape nor color-related traits signifying variation of considered traits were not from seed size. A normal distribution frequency have been observed for GL and b* traits while GW, L* and a* traits showed a bimodal distribution (**Figure 21**).

Table 12. Descriptive statistics for kernel shape and color-related traits in Ethiopian durum wheat accessions.

	GL^a (mm)	GW (mm)	L*	a*	b*
Mean	7.49	3.04	57.26	9.55	16.13
Maximum	8.70	3.57	67.78	13.19	20.89
Median	7.5	3.09	60.75	8.66	16.23
Minimum	5.99	2.44	43.52	6.53	11.05
StDev	0.50	0.26	7.40	2.00	2.40
P accessions^b	*	*	*	*	*

^a Kernel size and color trait acronyms: GL, Grain length; GW, Grain width; L*, brightness; a*, redness; b*, yellowness

^b Significance of the means between accessions; * P < 0.0



Figure 20. Correlation coefficient and level of significance between kernel size, shape and color traits in Ethiopian durum wheat accessions. Trait acronyms: GL, Grain length; GW, Grain width; TGW, thousand grain weight; L*, brightness; a*, redness; b*, yellowness

Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

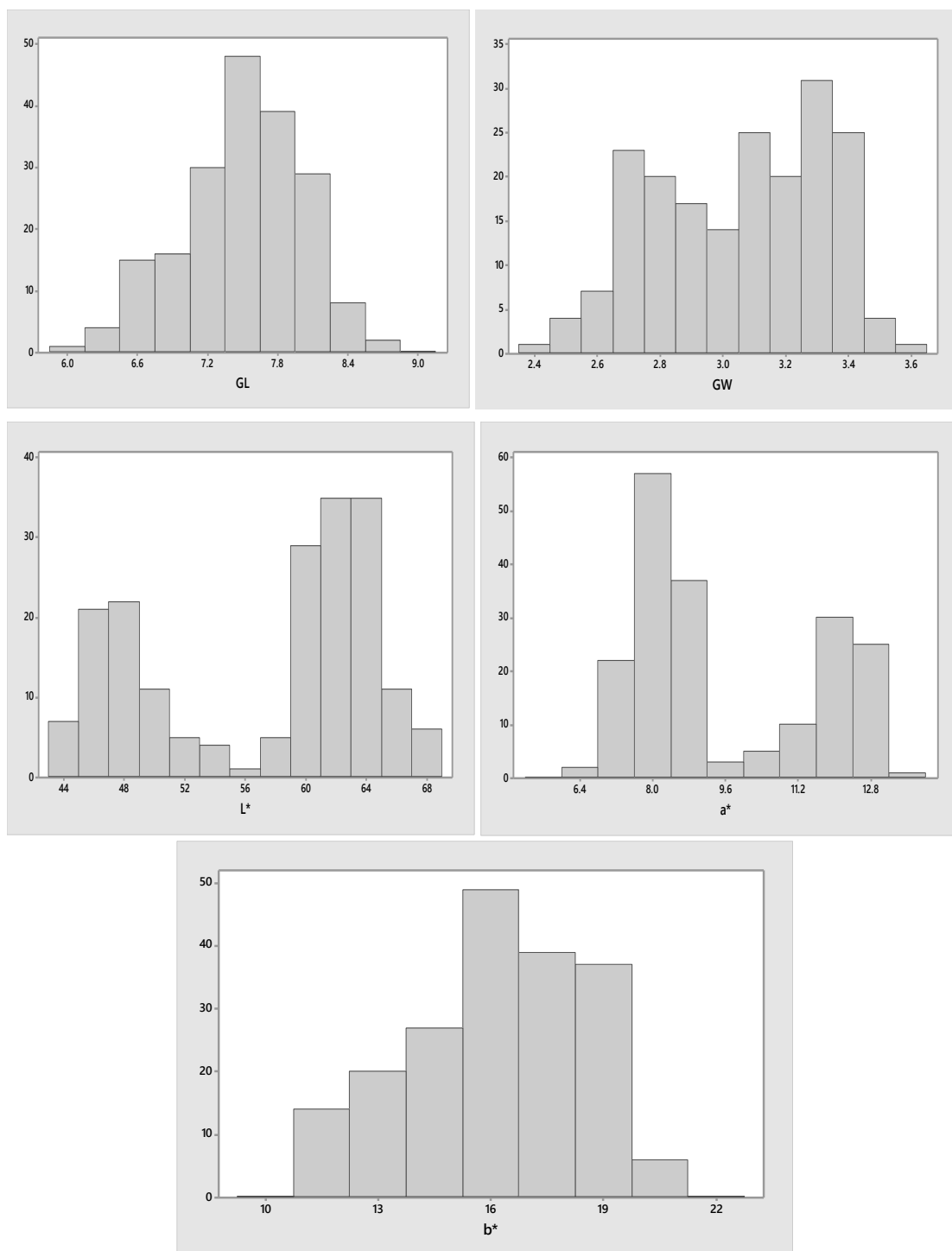


Figure 21. Distribution frequency for grain shape and color-related traits in Ethiopian durum wheat accessions. GL, grain length; GW, grain width; L*, brightness; a*, redness; b*, yellowness.

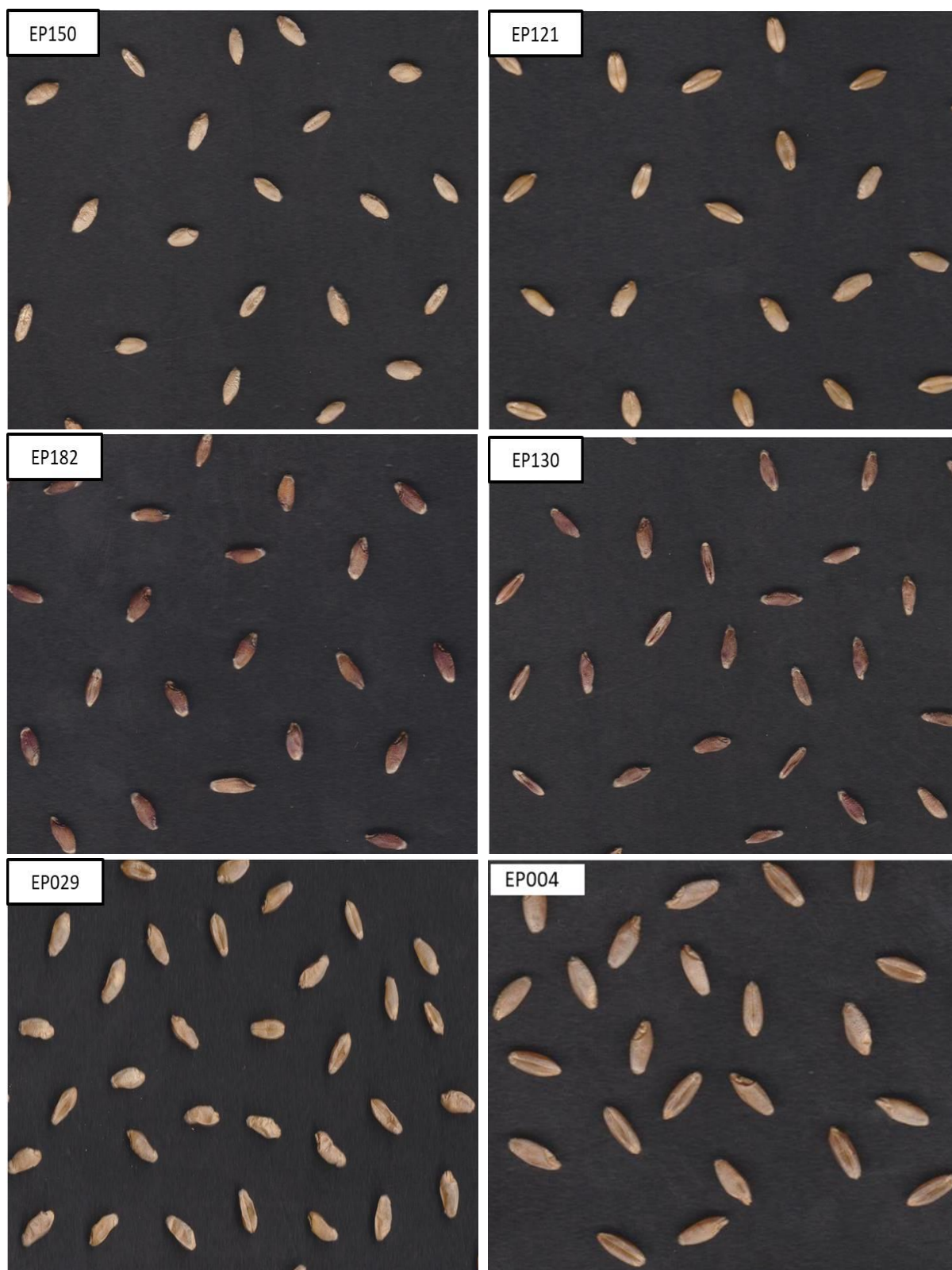


Figure 22. Images of accessions with highest values of CIE L* (EP150), b* (EP121), a* (EP182), GL (EP130), GW (EP029) and with amber color (EP004).

4.3.2. GWAS Results

Mixed linear model with population structure and kinship matrix as covariate (MLM+Q+K) was the preferred approach for MTA analysis as the quantile-quantile (Q-Q) plot shown that the observed values were closer to the expected distribution (**Figure 23**). All 10,789 polymorphic SNP markers (4,591 SNPs from A and 6,198 SNPs from B genomes) and phenotypic data of grain weight, shape and color related traits from 192 Ethiopian durum wheat accessions were used to conduct the marker-trait association (MTA) analysis. Population structure data resulted from 1,496 tag-SNPs ($r^2 = 0.5$) and kinship matrix data resulted from 4,842 tag-SNPs ($r^2 = 1$) were also used as a covariate in the MLM-GWAS analysis.

A total of 46 QTLs were identified for grain shape and color related traits. The only two major QTLs exceeded the $-\log P \geq 4$ were EPdwa*-2A and EPdwL*-2A.2, $-\log P$ values of 5.39 and 5.23 and phenotypic variance (r^2) of 11.4 and 11.0 %, respectively. Eighteen nominal QTLs were able to reach the $-\log P \geq 3$ threshold and of which 5 QTLs were identified for each of b* and GL, 4 QTLs for each of L* and GW with phenotypic variance ranging from 5.5 to 6.8 % (**Table 13**). The other 26 QTLs were identified as a suggestive QTLs with threshold of $-\log P \geq 2.5$ (**Appendix Table 9**).

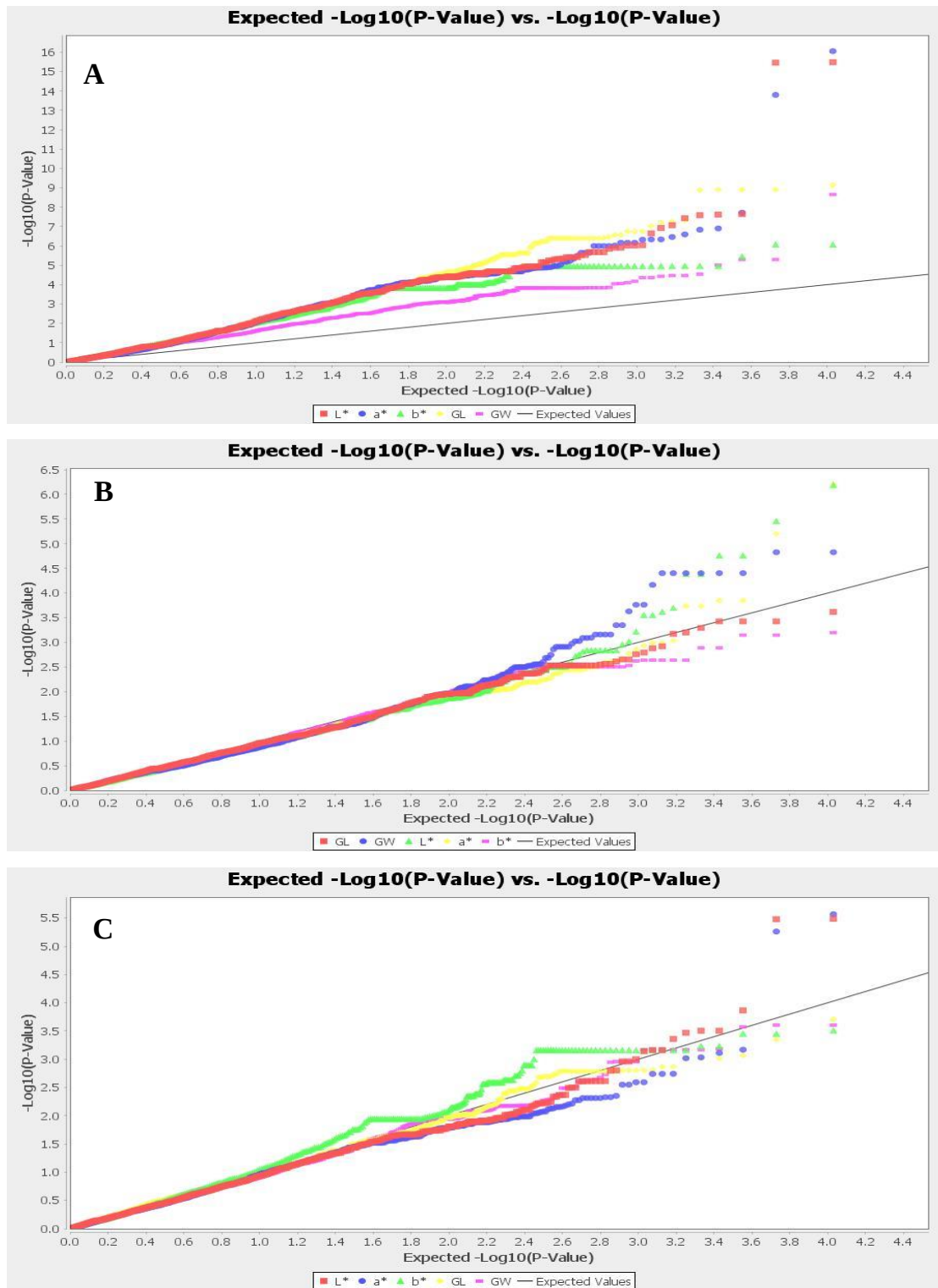


Figure 23. Quantile-quantile (Q-Q) plot of the GWAS analysis for grain shape and color related traits with different models: **A)** General Linear Model with population structure (GLM+Q); **B)** Mixed Linear Model with kinship matrix (MLM+K); **C)** Mixed Linear Model with population structure and kinship matrix (MLM+Q+K).

4.3.3. QTLs for Grain Length and Width

Five nominal QTLs (*EPdwGL-2B*, *EPdwGL-4B*, *EPdwGL-5A*, *EPdwGL-6A* and *EPdwGL-7B*) were detected for grain length on chromosomes 2B, 4B, 5A, 6A and 7B (**Table 13**). *EPdwGW-2A.1*, *EPdwGW-2A.2*, *EPdwGW-5A* and *EPdwGW-7B* were the four nominal QTLs detected for grain width on chromosomes 2A (2), 5A and 7B. Moreover, 11 additional suggestive QTLs were identified for GL and GW (**Figure 24**). Allelic distribution with their effect for QTL-tagging SNPs is reported in **Appendix Table 10** and **11** for GL and GW, respectively.

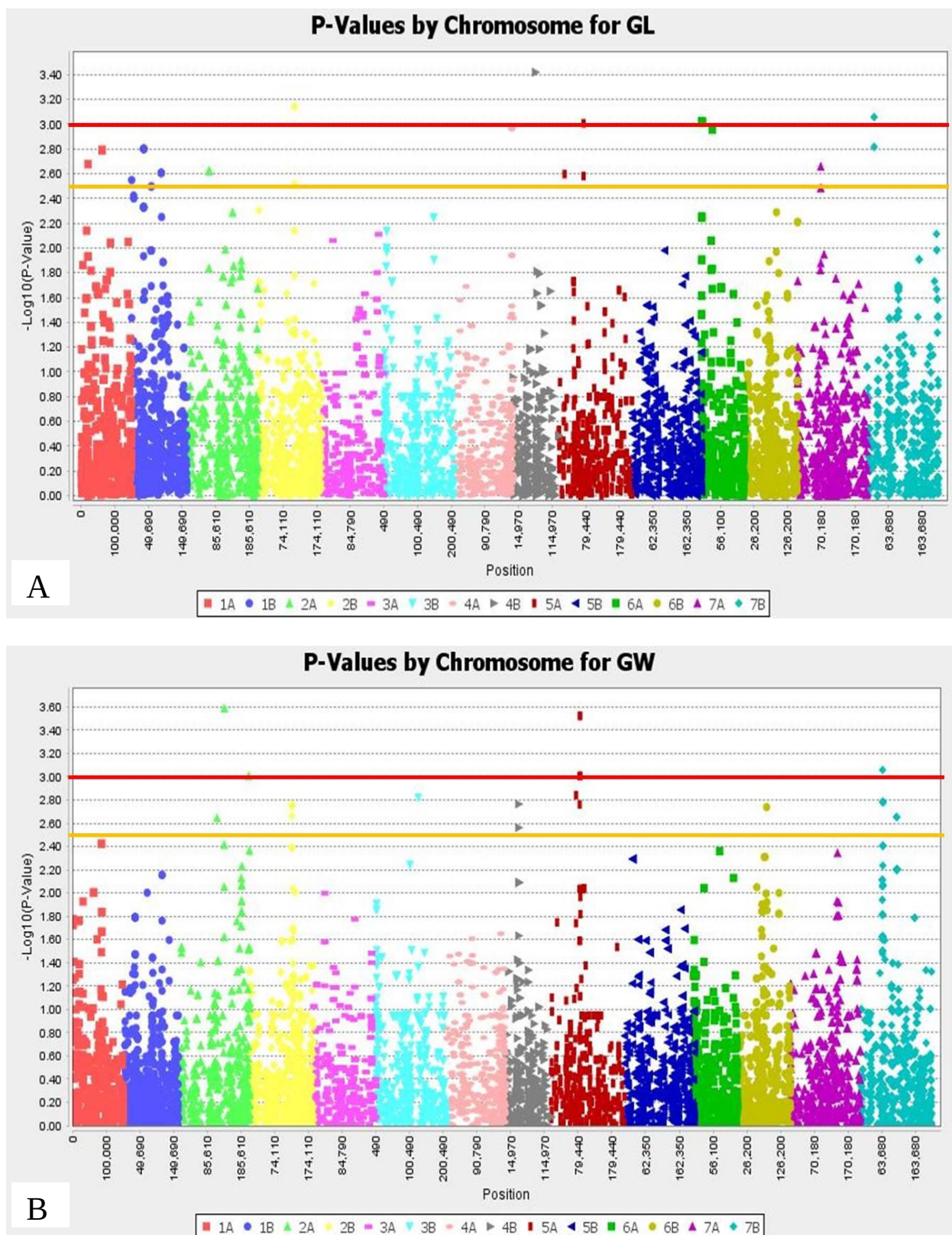
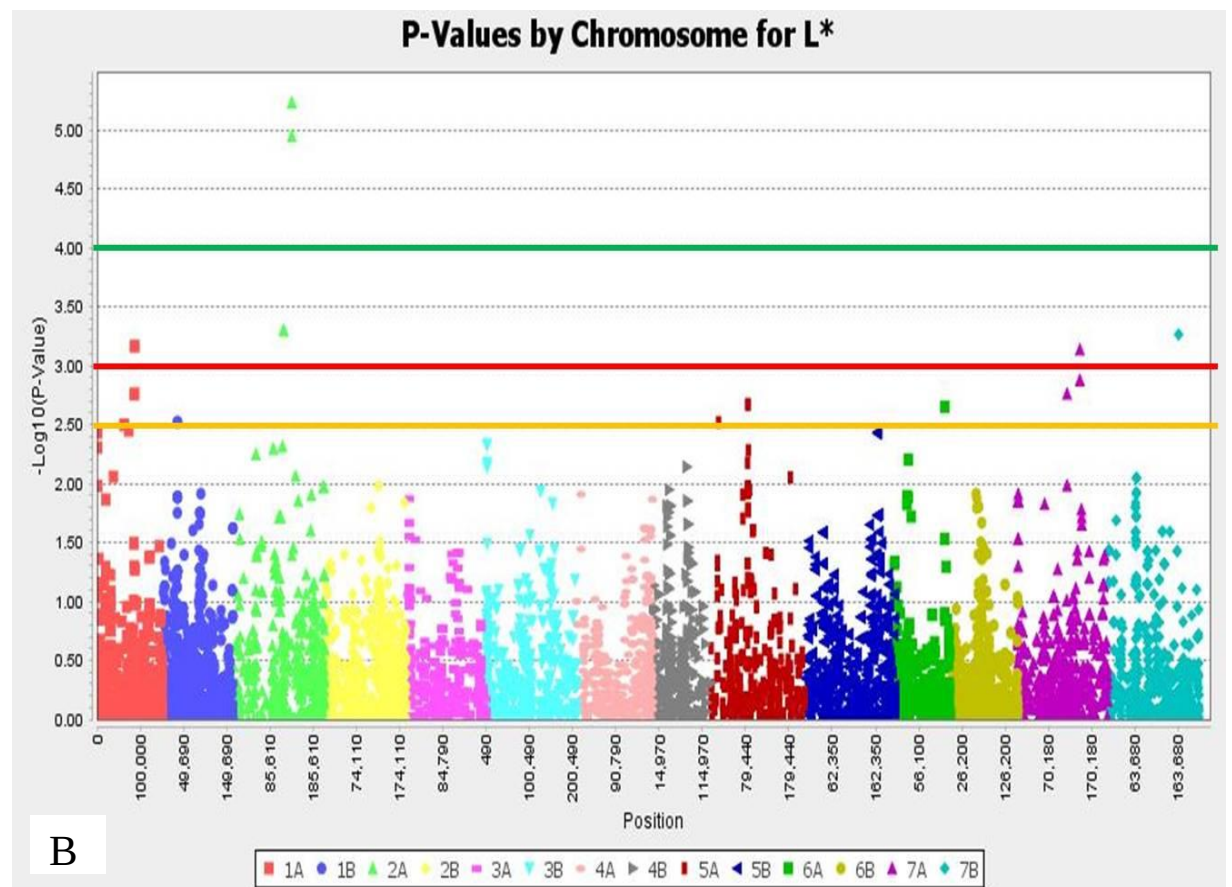
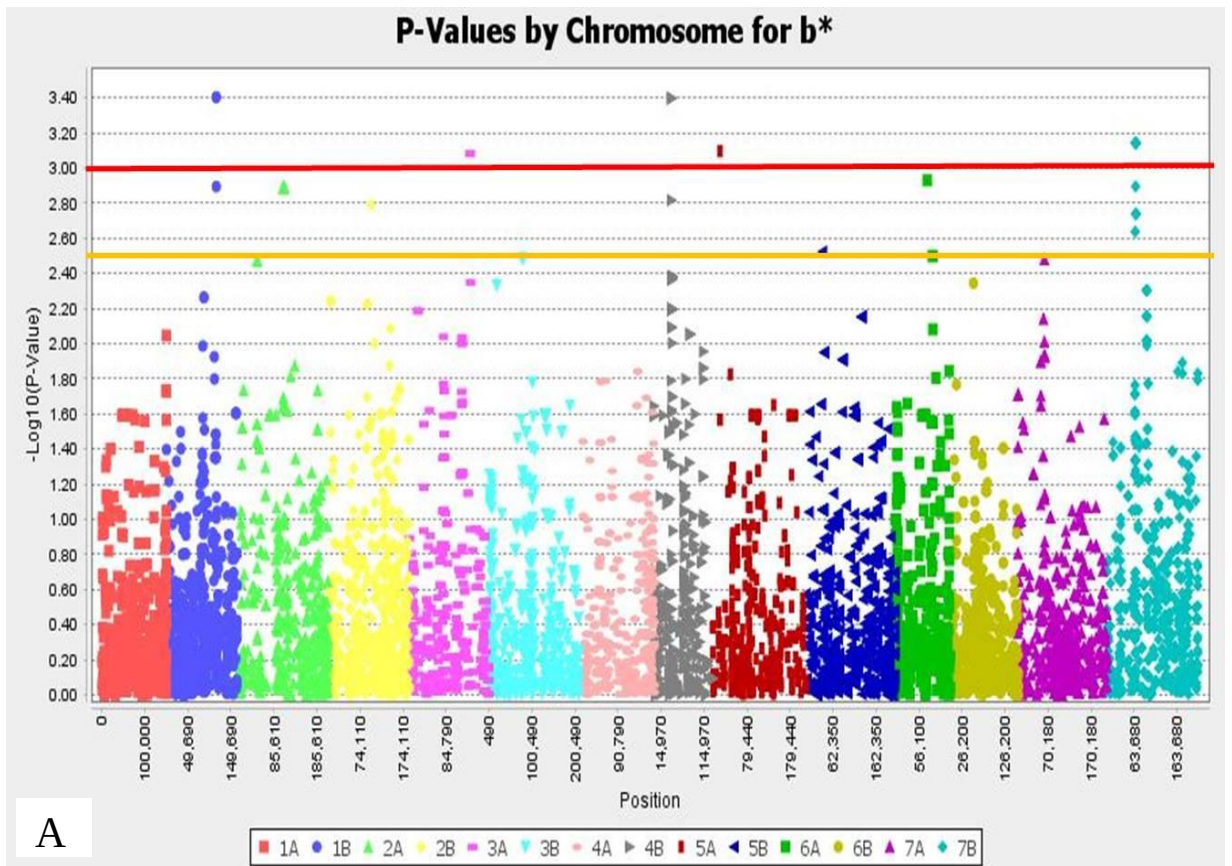


Figure 24. Manhattan plot specifying genomic regions with their significant MTA with grain length (**A**) and grain width (**B**) in 192 Ethiopian durum wheat accessions. The orange, red and green horizontal lines designates the significant association thresholds for suggestive ($-\log_{10} P \geq 2.5$), nominal ($-\log_{10} P \geq 3$) and major ($-\log_{10} P \geq 4$) QTLs, respectively.

4.3.4. QTLs for Color-related Traits

A major QTL with a positive effect for a^* (redness) ($EPdwa^*-2A$) and a negative effect for L^* (brightness) ($EPdwL^*-2A.2$) was identified at a single locus (*IWB72154*, QTL-tag SNP) on the long arm of chromosome 2A with a slightly higher significance for a^* ($-\log P = 5.39$) than L^* ($-\log P = 5.23$) (**Figure 25**) and explained 11.4 and 11.0 % phenotypic variance, respectively. This QTL also showed a pleiotropic effect for grain width (**Figure 26**). Closer to this major QTL, another single locus (*IWB8286*, QTL-tag SNP) made a nominal QTL for L^* ($EPdwL^*-2A.1$) with negative effect and suggestive QTL for a^* with positive effect. Additional four nominal QTLs ($EPdwL^*-1A$, $EPdwL^*-2A.1$, $EPdwL^*-7A$ and $EPdwL^*-7B$) were also detected for L^* on chromosomes 1A, 2A, 7A and 7B. Moreover, five nominal QTLs, $EPdwb^*-1B$, $EPdwb^*-3A$, $EPdwb^*-4B$, $EPdwb^*-5A$ and $EPdwb^*-7B$, were detected for b^* (yellowness) on chromosomes 1B, 3A, 4B, 5A and 7B, respectively. Additional 10 suggestive QTLs spotted for L^* . a^* and b^* traits are reported in **Appendix Table 9**. The allelic distribution and frequency of b^* , L^* and a^* QTL-tagging SNPs is reported in **Appendix Tables 12, 13 and 14**, respectively.



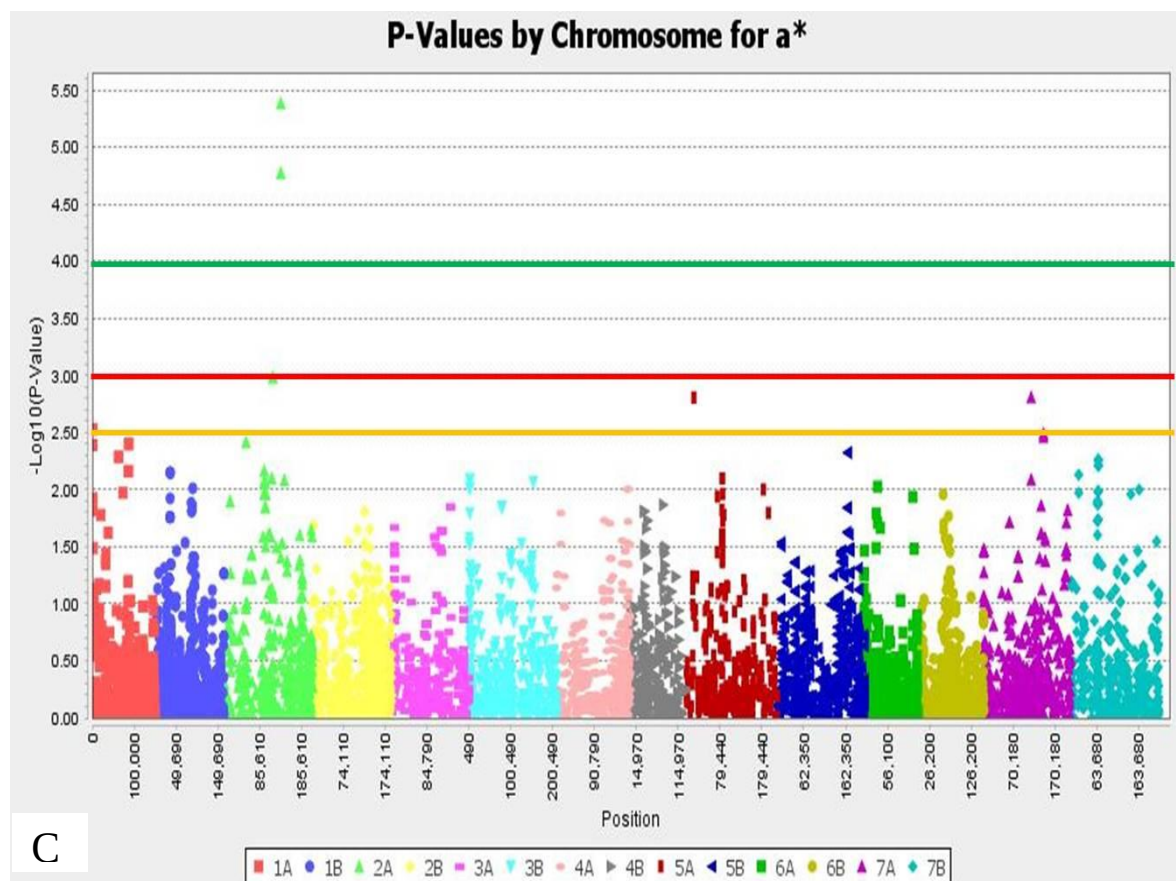


Figure 25. Manhattan plot specifying MTA with yellowness (**A**), brightness (**B**) and redness (**C**) traits in Ethiopian durum wheat accessions. The orange, red and green horizontal lines designates the significant association thresholds for suggestive ($-\log_{10} P \geq 2.5$), nominal ($-\log_{10} P \geq 3$) and major ($-\log_{10} P \geq 4$) QTLs, respectively.

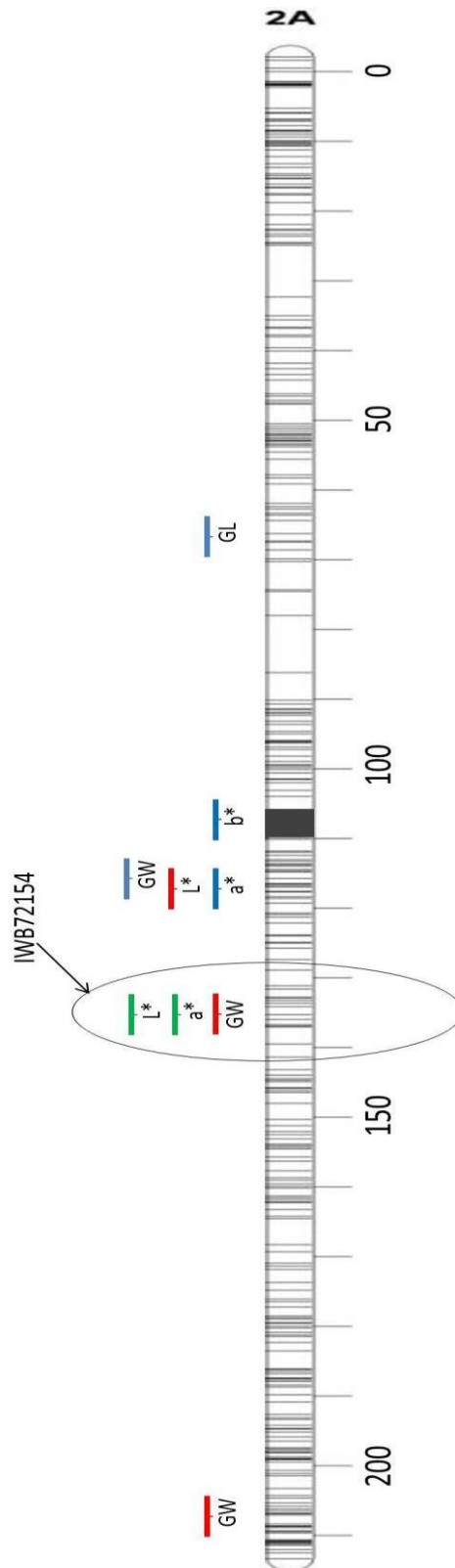


Figure 26. A major QTL (*IWB72154*, the QTL-tag SNP) identified on the long arm of chromosome 2A with a positive effect for CIE a^* and negative effect for CIE L^* .

Table 13. List of identified QTLs for kernel shape and color traits in Ethiopian durum wheat.

QTL	Trait ^a	Marker ^b	Chr	Position (cM)	P-value	P(- log10)	R ² (%)	Sig. SNPs ^c	CI (cM) ^d	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
<i>EPdwa*-2A</i>	a*	<i>IWB72154</i>	2A	5.39	0.000004	5.39	11.4	1	133.79-138.29	C	1.36	104	T	0	88
<i>EPdwb*-1B</i>	b*	<i>IWB11958</i>	1B	115.74	0.000395	3.40	6.3	2	113.49-117.99	C	1.32	147	T	0	45
<i>EPdwb*-3A</i>	b*	<i>IWB11992</i>	3A	141.52	0.000828	3.08	5.6	1	139.27-143.77	A	1.46	61	G	0	131
<i>EPdwb*-4B</i>	b*	<i>IWB73411</i>	4B	39.47	0.000401	3.40	6.3	4	37.22-41.72	C	-1.45	22	T	0	170
<i>EPdwb*-5A</i>	b*	<i>IWA3196</i>	5A	16.83	0.000802	3.10	5.7	0	14.58-19.08	C	4.66	26	T	0	166
<i>EPdwb*-7B</i>	b*	<i>IWB34768</i>	7B	67.34	0.000721	3.14	5.8	11	65.09-69.59	C	1.28	55	T	0	137
<i>EPdwL*-1A</i>	L*	<i>IWB65551</i>	1A	87	0.000683	3.17	6.0	3	84.75-89.25	C	5.19	115	T	0	77
<i>EPdwL*-2A.1</i>	L*	<i>IWB8286</i>	2A	117.05	0.000501	3.30	6.3	1	114.8-119.3	C	-5.35	43	T	0	149
<i>EPdwL*-2A.2</i>	L*	<i>IWB72154</i>	2A	136.04	0.000005	5.23	11.0	1	133.79-138.29	C	-4.96	104	T	0	88
<i>EPdwL*-7A</i>	L*	<i>IWB72494</i>	7A	143.19	0.000729	3.14	5.9	1	140.94-145.44	G	7.48	167	T	0	25
<i>EPdwL*-7B</i>	L*	<i>IWB62029</i>	7B	165.05	0.000545	3.26	6.2	0	162.8-167.3	C	6.66	182	T	0	10
<i>EPdwGL-2B</i>	GL	<i>IWB3865</i>	2B	108.92	0.000723	3.14	6.1	4	106.67-111.17	c	-0.37	102	T	0	90
<i>EPdwGL-4B</i>	GL	<i>IWB9672</i>	4B	66.43	0.000381	3.42	6.8	0	64.18-68.68	C	0.67	38	T	0	154
<i>EPdwGL-5A</i>	GL	<i>IWB43493</i>	5A	72.73	0.000985	3.01	5.8	1	70.48-74.98	C	-0.45	50	T	0	142
<i>EPdwGL-6A</i>	GL	<i>IWB67412</i>	6A	1.06	0.000955	3.02	5.8	14	0-3.31	A	-0.39	141	G	0	51
<i>EPdwGL-7B</i>	GL	<i>IWA2568</i>	7B	20.75	0.000877	3.06	5.9	1	18.5-23	A	-0.55	159	G	0	33
<i>EPdwGW-2A.1</i>	GW	<i>IWB72154</i>	2A	136.04	0.000258	3.59	6.8	0	133.78-138.29	C	-0.15	104	T	0	88
<i>EPdwGW-2A.2</i>	GW	<i>IWB23912</i>	2A	208.76	0.000985	3.01	5.5	0	206.51-211.01	C	-0.32	31	T	0	161
<i>EPdwGW-5A</i>	GW	<i>IWB46350</i>	5A	84.77	0.000300	3.52	6.6	8	82.52-87.07	A	-0.20	114	G	0	78

Table 13. Continued

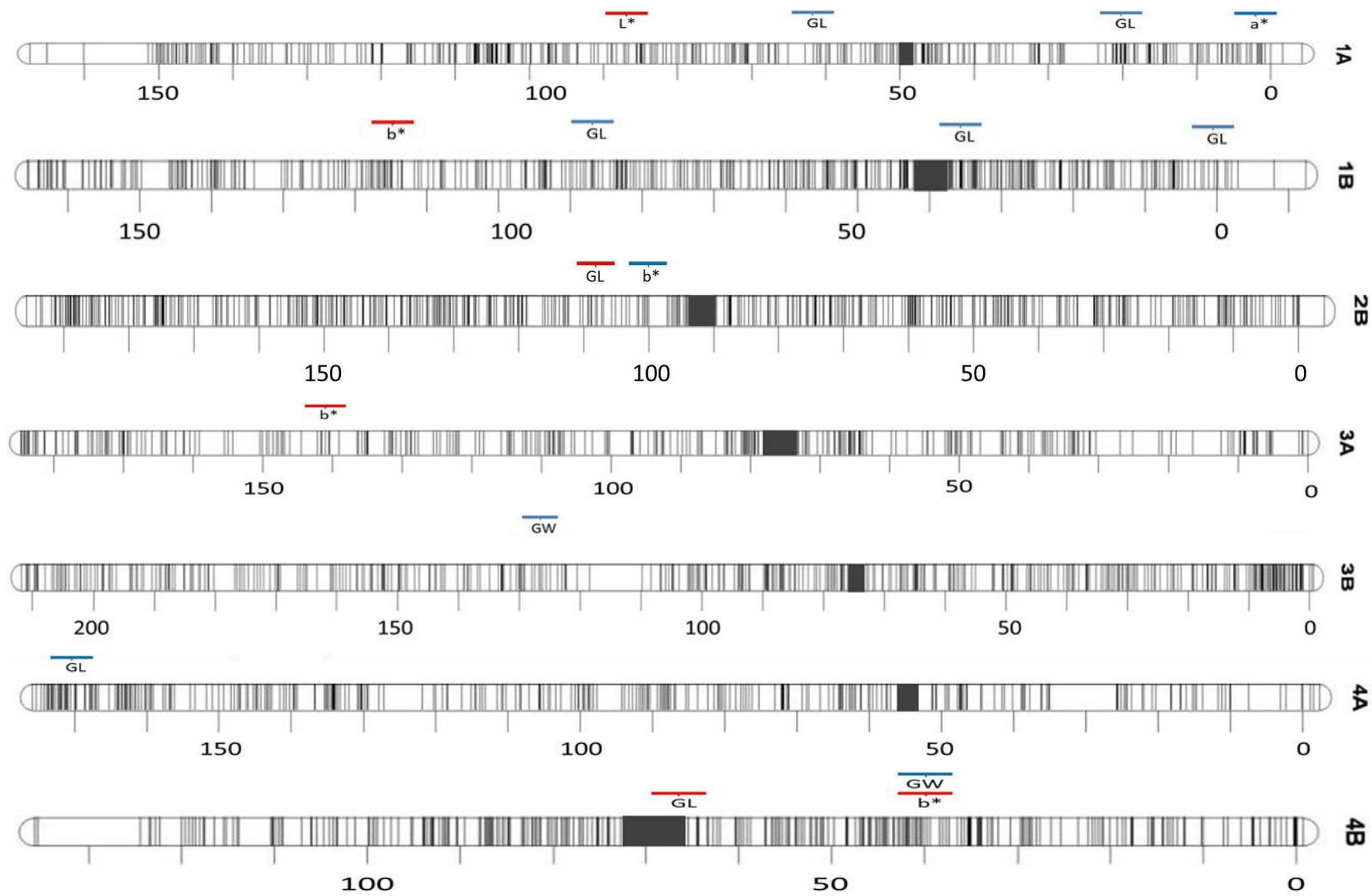
QTL	Trait ^a	Marker ^b	Chr	Position (cM)	P-value	P(- log10)	R ² (%)	Sig. SNPs ^c	CI (cM) ^d	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
<i>EPdwGW-7B</i>	GW	<i>IWB36189</i>	7B	66.36	0.000874	3.06	5.6	7	64.11-68.61	A	-0.15	137	G	0	55

^a Trait acronyms: GL, Grain length; GW, Grain width; L*, brightness; a*, redness; b*, yellowness

^b A SNP found at the peak of corresponding QTL (QTL-tag SNP).

^c The number of significant SNPs existed in the significant interval.

^d Confident interval from the left and right of QTL-tag SNP based on the tetraploid wheat consensus map (Maccaferri *et al.*, 2015)



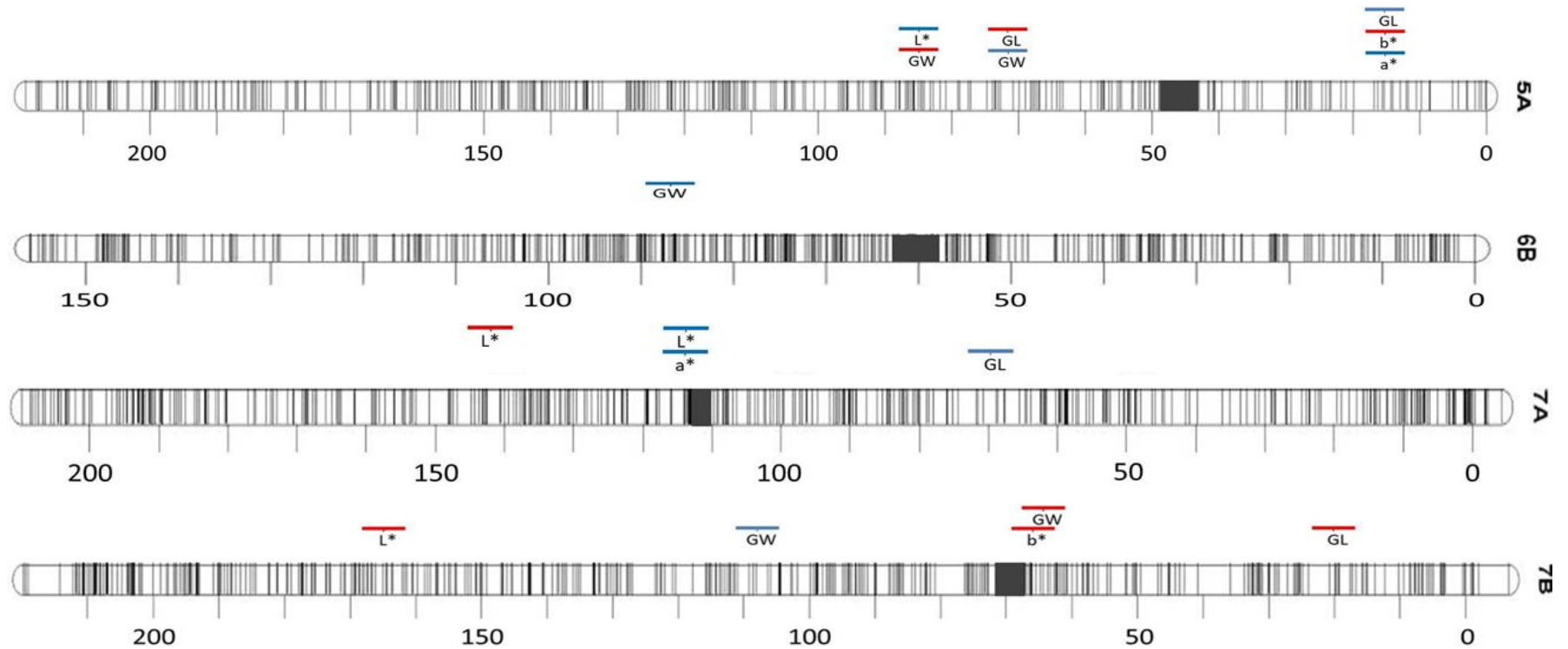


Figure 27. Genetic map of QTLs identified for grain shape and color-related traits in 192 Ethiopian durum wheat accessions projected onto the SNP-based tetraploid consensus map Maccaferri *et al.* (2015). QTLs are listed on the left of chromosomes with different colored bars representing their significance (blue bars for $-\log p \geq 2.5$ (suggestive QTLs); red bars for $-\log p \geq 3$ (nominal QTLs); and green bars for $-\log p \geq 4$ (major QTLs) . The length of bars indicates the confidence interval of QTLs and the horizontal line indicates the position of QTL-tagging SNPs. Trait acronyms: GL, grain length; GW, grain width; L*, brightness; a*, redness; b*, yellowness.

5. DISCUSSION

5.1. Genetic Diversity, Linkage Disequilibrium and Population Structure

Genetic diversity analysis is a crucial step in spotting the existing novel alleles that could be used as source of novel traits which are high yielding, resilient for biotic and/or abiotic stresses and yet delivers satisfied productivity or in meeting the end user demands in plant breeding. Ethiopian durum wheat landraces have specially proven to show a relevant variation for various traits that comes from their potential to adapt to changing environmental conditions (Tesfaye *et al.*, 1993). Due to this, Ethiopian durum wheat germplasm has served as a center of focus for genetic studies and source of novel QTLs, genes and gene complexes for many traits (Sakamoto and Fukui, 1972; Porceddu *et al.*, 1973; Pecetti *et al.*, 1992; Haile *et al.*, 2013; Mengistu *et al.*, 2016; Liu *et al.*, 2017; Maccaferri *et al.*, 2019).

Slightly higher number of SNPs (30,510) were reproduced in the present study from the 90K wheat SNP array than previously reported by Mengistu *et al.* (2016) on Ethiopian durum wheat panel (30,155 SNPs) and in Mediterranean durum wheat collections (21,069 SNPs). Genomes of A and B did not show significant difference in diversity indices, indicating that they have followed similar evolutionary histories in Ethiopian landraces and improved varieties (Mengistu *et al.*, 2016). The 90K wheat SNP array was a platform made to capture the most reliable gene-associated SNP markers available in wheat genome worldwide and could not enable to mine new loci. Hence, the less number of SNPs reproduced from the array in the present study indicates the presence of novel alleles in Ethiopian durum wheat and further studies will benefit from the employment of both hybridization and sequencing methods to

provide a thorough description of Ethiopian wheat molecular genetic diversity (Mengistu *et al.*, 2016).

Comparing with previous reports, higher genetic diversity indices were scored in Ethiopian durum wheat panel (**Table 3**) that strengthens the unresolved arguments of Ethiopia as center of origin and/or diversity of this crop. For instance, Ren *et al.* (2013) reported mean polymorphic information content (0.18) and Nei's gene diversity (0.22) from world-wide collected 150 durum wheat accessions genotyped with 1536 SNP markers. Kabbaj *et al.* (2017) obtained a mean PIC values of 0.119 from 337 durum wheat accessions composed of landraces, varieties and elite lines collected from more than 30 countries and genotyped with 35K Affymetrix Axiom wheat breeders array. Eltaher *et al.* (2018) reported slightly higher mean gene diversity (0.3) and PIC (0.23) in 250 winter wheat accessions genotyped with Genotyping-By-Sequencing (GBS) platform. However, unlike the present study, they only included SNP markers having less than 20% missing information and with minor allelic frequency (MAF) > 0.05. Higher PIC and genetic diversity scores were reported in studies using multi-allelic markers such as SSR (Maccaferri *et al.*, 2003; Moragues *et al.*, 2007).

Genetic stratification analysis based on the Bayesian clustering model of the second order rate of change of the likelihood (Evanno *et al.*, 2005) revealed the presence of three optimal subpopulations. However, discriminant analysis of principal components (DAPC) based on the Bayesian information criterion (BIC) couldn't show the smallest BIC on a specific K value above which all the BIC values spontaneously decreased and then started a spontaneous increments creating an elbow

shape (Jombart *et al.*, 2010). However, it provided a clue in which somehow less than 5 clusters could be optimal. Varieties showed a single distinct cluster and landraces distributed in to two additional clusters. Both principal component analysis (PCA) using the first two components and the neighbor joining clustering based on simple matching dissimilarity coefficient proved the former clustering result could be optimal by showing a three clear clusters. In the current study, clustering was not based on their geographic origin where accessions were originally collected in Ethiopia. Mengistu *et al.* (2016) reported similar result on a study conducted in 311 Ethiopian durum wheat accessions (287 landraces and 24 varieties) collected from major wheat producing areas of the country. The basic reason for this admixture could be the existence of historical exchange of seeds through an informal seed system involving regional and countrywide farming communities (Seboka and Deressa, 1999). Ren *et al.* (2013) reported neither geographical nor ecological evidence was detected in grouping 150 durum wheat accessions with world-wide origin and noted that the reason might be that the gene flows via germplasm exchanges among different regions occurred frequently or that human transfer of genes in history made a very big admixture. Kabbaj *et al.* (2017) found higher admixture between 370 durum wheat accessions of landraces, varieties and elite lines collected from more than 30 countries including Ethiopia. However, they observed a very limited admixture between Ethiopian landraces with other collections originated world-wide and Ethiopian durum wheat landraces made a separate cluster and proved the presence of a unique morphology (Sakamoto and Fukui, 1972; Pecetti *et al.*, 1992) and represent a separate sub-species under the name *Triticum durum* subs. *abyssinicum* or *T. aethiopicum* (Mengistu *et al.*, 2015, 2016). This phenomena placed Ethiopia as a secondary center

of origin and/or diversity for durum wheat since the germplasm is distinct from the primary origin of durum wheat (Levantine countries) (Kabbaj *et al.*, 2017).

5.2. Genome-Wide Association Analysis for Seminal Root System Architecture Traits

Scientists acknowledged the enormous impact of roots in both water and nutrition acquisition in many crop plants long time ago but quantification and selection of appropriate root traits in breeding programs have not been intensively studied (Waines and Ehdaie, 2007). The basic reason for limited research effort in roots so far is fundamentally the difficulty in phenotyping root system architectural traits in different crop plants. Nonetheless, a better understanding of root functional traits and their relation to whole plant strategies is necessary to increase crop productivity under different unfavorable conditions. Previous QTL studies on seminal RSA traits of wheat and other crops have proven their predictive ability for root morphology grown in field plants (Tuberosa *et al.*, 2002; Landi *et al.*, 2010; Mace *et al.*, 2012; Cane *et al.*, 2014; Li *et al.*, 2015; Richard *et al.*, 2015; Uga *et al.*, 2015; Maccaferri *et al.*, 2016; Ren *et al.*, 2017). Seminal RSA traits could predict the mature root system (Liao *et al.*, 2004), as established by correlation analysis and co-located QTL identification (An *et al.*, 2006; Atkinson *et al.*, 2015; Maccaferri *et al.*, 2016). Characterizing RSA traits in mature field-grown crops is enormously tough and different seminal RSA phenotyping platforms have emerged in order to evaluate root morphology under controlled conditions as proxy for field performance (Zhu *et al.*, 2005; Laperche *et al.*, 2006; Ren *et al.*, 2012; Liu *et al.*, 2013; Cane *et al.*, 2014; Iannucci *et al.*, 2017).

Wheat has a dense fibrous root system, which is difficult to quantify and to select directly by breeders. Therefore, mapping QTL for root traits and developing marker-assisted selection will help breeders to select root traits desirable for efficient acquisition of water and nutrients from soils (Ren *et al.*, 2012).

In the present study, 192 Ethiopian durum wheat accessions (predominantly landraces) were phenotyped for different RSA traits using a paper non-roll with a polycarbonate plate in growth chamber. Moderate to higher heritability, ranging from 67 - 91%, was recorded for RSA traits that make selection of favorable root traits as a feasible approach for improvement. However, it is obvious that this kind of phenotyping method in controlled environment creates a homogeneous root environment across accessions, replications and blocks unlike in the field in which the rhizosphere environment is highly heterogeneous, significantly reducing heritability.

RSA traits from 12-day-old seedlings grown using only distilled water were used to spot QTLs through GWAS analysis. Novel SNP marker platforms have had a great application in QTL detection and genomic-assisted selection in wheat (Tuberosa and Pozniak, 2014). The 90K wheat SNP array by Illumina enables a highly accurate genome-wide scans that greatly facilitates and enhances the accuracy of comparative analysis and QTL cross-referencing (Wang *et al.*, 2014; Maccaferri *et al.*, 2015). The analysis of linkage disequilibrium (LD) using 10,789 polymorphic SNPs from the 90K wheat SNP array indicated that LD decays to the threshold value of $r^2 = 0.3$ (the generally accepted limit to detect association with a QTL) at 2.25 cM that is previously detected with Liu *et al.* (2017) with the same panel but less with 10 accessions. Maccaferri *et al.* (2014; 2015) indicated the LD decays at 2.20 cM for the

panel comprising 183 elite durum wheat varieties and lines from Mediterranean countries, the Southwestern USA, and Mexico.

Clear RSA QTL-clusters identified throughout all chromosomes, represented as either single causal loci with a pleiotropic effect on different RSA traits or as tightly linked loci not resolved by recombination (Tuberosa *et al.*, 2002), and of which most of them are overlapped with previously identified RSA QTL clusters/hotspots.

Root length and number at the seedling stage are potential candidates for marker-assisted breeding applications aimed at enhancing early rooting capacity (Maccaferri *et al.*, 2016). One novel QTL for TRN, EPdwTRN-4A, was discovered in the present study on the short arm of chromosome 4A. The other TRN QTL was identified on the short arm of chromosome 1A that overlaps with a TRN-QTL reported by Maccaferri *et al.* (2016). In addition, TRN QTL spotted on the short arm of chromosome 1B overlapped with the confidence interval of TRN QTL identified by Christopher *et al.* (2013). Other nominal TRN QTLs identified on chromosome 4BS overlapped with a QTL reported by Ren *et al.* (2012) and long arm of chromosome 4B and short arm of chromosome 7A both overlapped with a QTL reported in Maccaferri *et al.* (2016) for the same trait. Chromosome 4B showed three strong QTLs (EPdwRT6-4B.1, EPdwRT6-4B.2 and EPdwRT6-4B.3) for the presence of more than five seminal roots per plant (RT6). These RT6-QTLs appeared as a cluster with TRN that indicates the allele has a positive effect on the root number.

Root length is the other essential trait and three nominal QTLs were identified for TRL and one for ARL. One novel QTL for TRL, EPdwTRL-4B, was spotted in the

present study on the long arm of chromosome 4B. TRL QTL identified on the short arm of chromosome 1B overlaps with a study reported by Petrarulo *et al.* (2015) and Liu *et al.* (2013) for the same trait and the other QTL detected at telomeric region of chromosome 5A overlapped with a QTL reported by Maccaferri *et al.* (2016). A nominal ARL QTL identified on chromosome 2A, that had also a pleiotropic effect on TRL, SDW, RDW, and IRW, have never been reported in any of the previous studies projected here in the tetraploid consensus map published by Maccaferri *et al.* (2015).

The other crucial RSA trait is root growth angle (RGA) and one major QTL, EPdwRGA-6A, with higher phenotypic effect was identified on the long arm of chromosome 6A. This QTL (with the same haplotype) was also detected by Maccaferri *et al.* (2016), QRga.ubo-6A.2, using 183 elite varieties and lines from Mediterranean countries, the Southwestern USA, and Mexico for the same trait. Along with this major QTL, five adjacent RGA QTLs were spotted making a unique RGA-QTL-cluster on the long arm of chromosome 6A. Considering the major effect and overlapping with the previous study, conducting further validation of the haplotype for this candidate QTL could be a worthy action. One novel nominal RGA QTL was identified on the long arm of chromosome 4A.

Bulk root and shoot dry weight and individual dry root weight (inferred through dividing the bulk dry root weight by total root number and could be used as a proxy to measure root thickness) are the other investigated RSA traits. In the present study, varieties performed better than landraces in both root and shoot dry weight. These traits were appeared as a QTL clusters in many occasions. These RSA QTLs showed a clear cluster at QTL-clusters 2, 3, 6, 7, 9, 10 and 14 of which some are overlapped

with QTLs reported in previous studies for the same trait (Laperche *et al.*, 2006; Kubo *et al.*, 2007; Guo *et al.*, 2012; Maccaferri *et al.*, 2016) and some are newly discovered. A novel major RDW QTL (EPdwRDW-4A), that has also a pleiotropic effect on SDW, TRN, and TR6, was discovered on the short arm of chromosome 4A. Other novel RDW QTL (EPdwRDW-3A) was also detected on the long arm of chromosome 3A. EPdwSDW-3B and EPdwSDW-4A were the two newly discovered nominal SDW QTLs at the short arm of chromosome 3B and long arm of chromosome 4A, respectively. Four novel IRW QTLs (EPdwIRW-5B.1, EPdwIRW-5B.2, EPdwIRW-6B, EPdwIRW-7A) were discovered on the short arm of chromosome 5B (the first two), long arm of chromosome 6B and short arm of chromosome 7A, respectively. Iannucci *et al.* (2017) stated the absence of a clear relationship between plant height and root development so far and added a diverse and controversial speculations from a number of previous studies, which are probably due to the different conditions and growth stages in which the root traits evaluated. Some of which reported a different sets of genetic loci control shoot and root growth (Sanguineti *et al.*, 2007; Wojciechowski *et al.*, 2009; Narayanan *et al.*, 2014) while others indicate a negative correlation (Kabir *et al.*, 2015). Bai *et al.* (2013) investigated a set of NILs for a number of Rht loci/alleles and showed clear effects in both shoot and root traits.

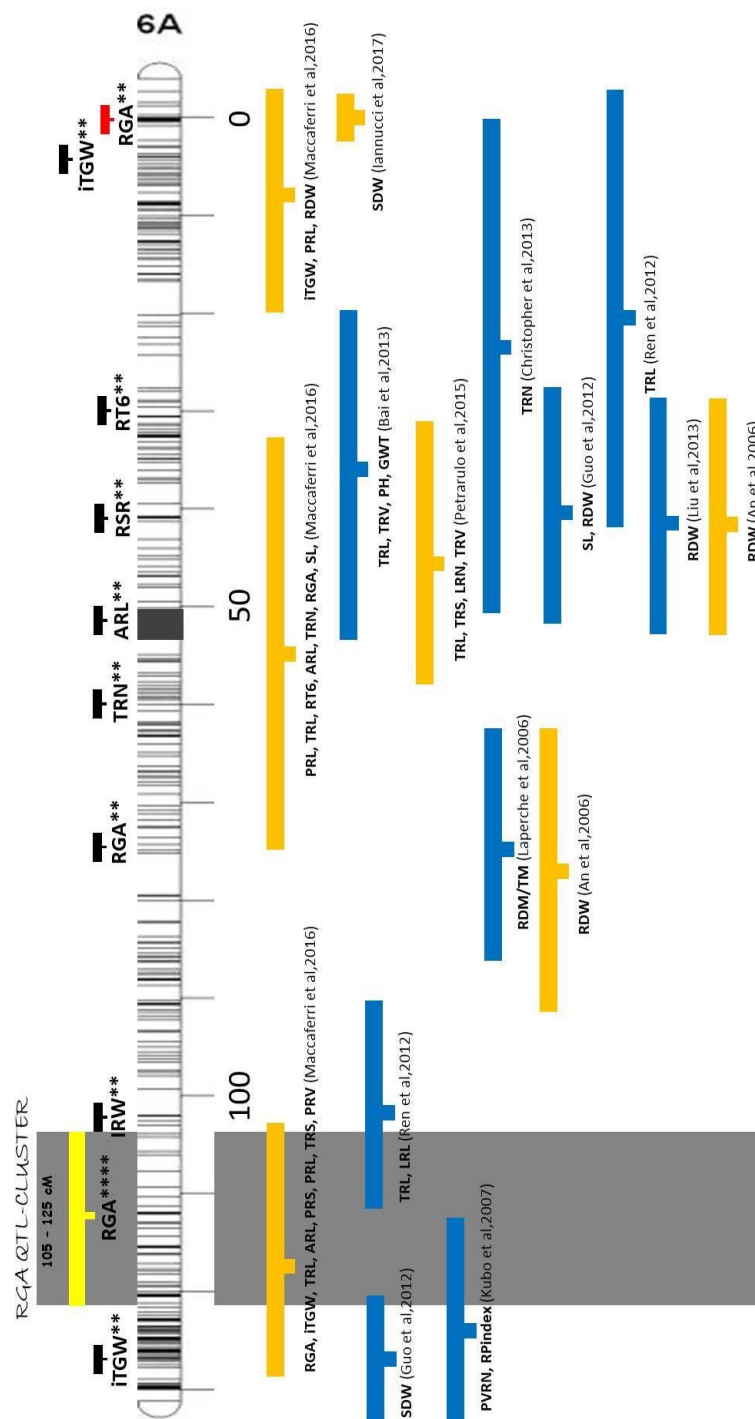
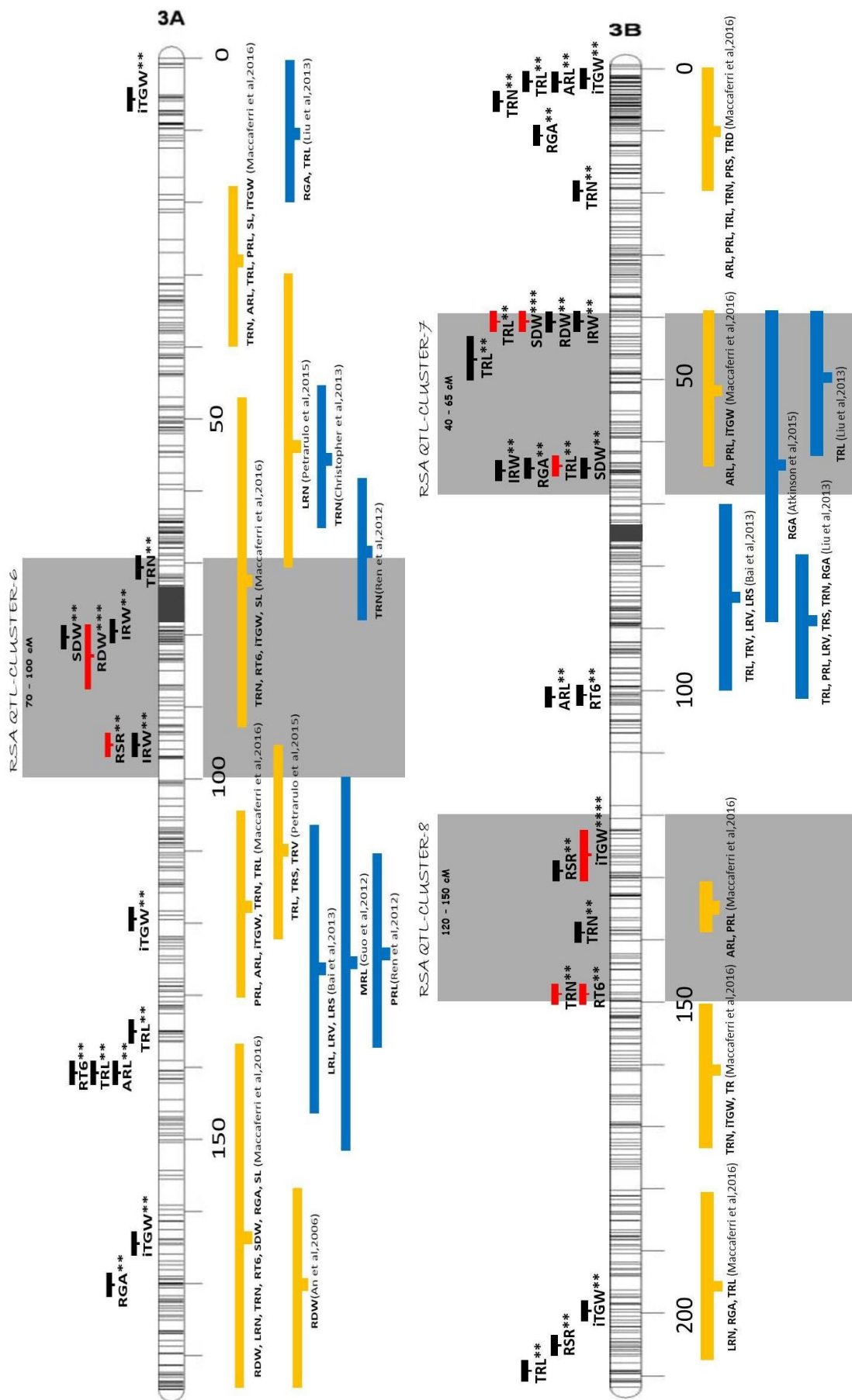
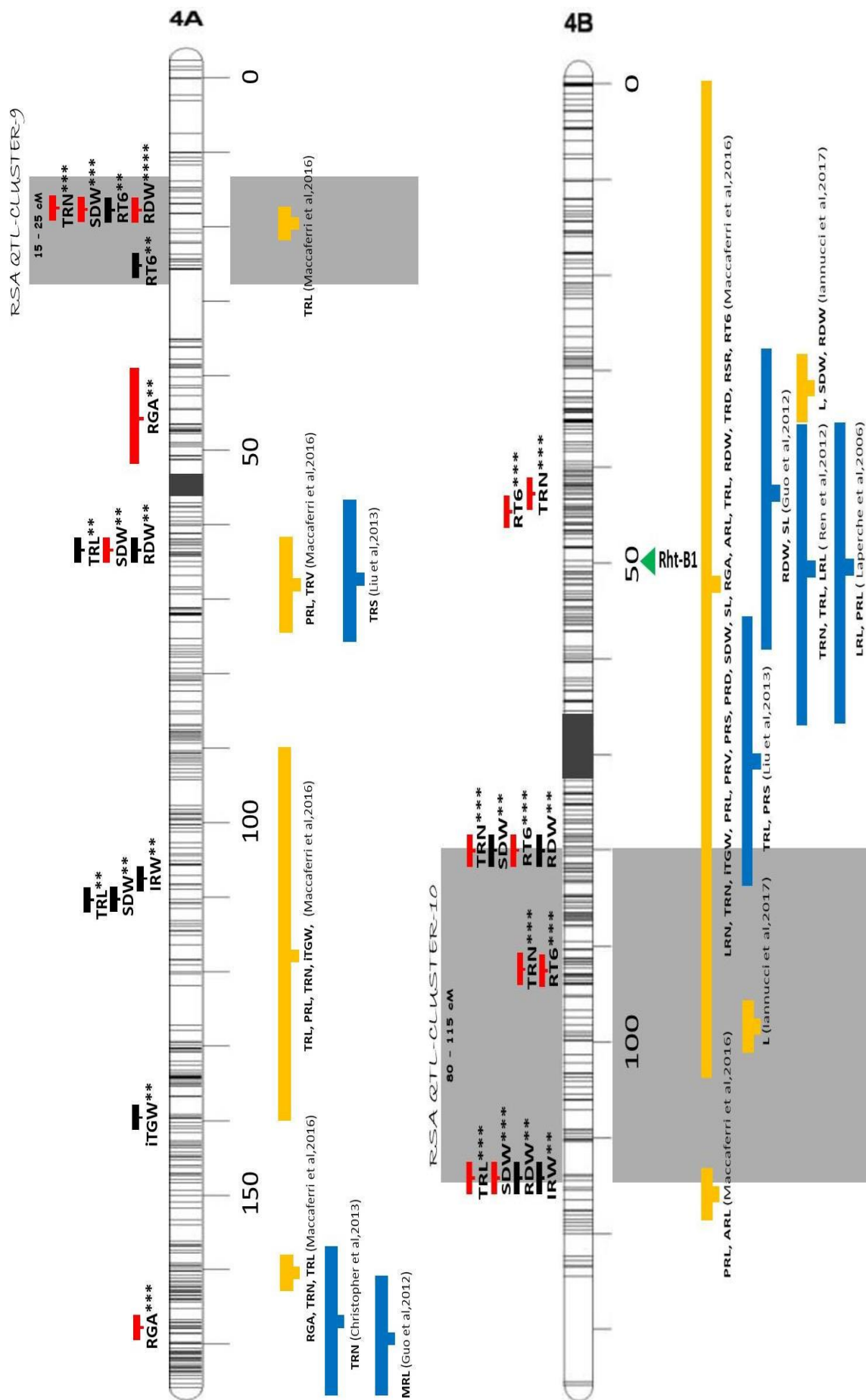
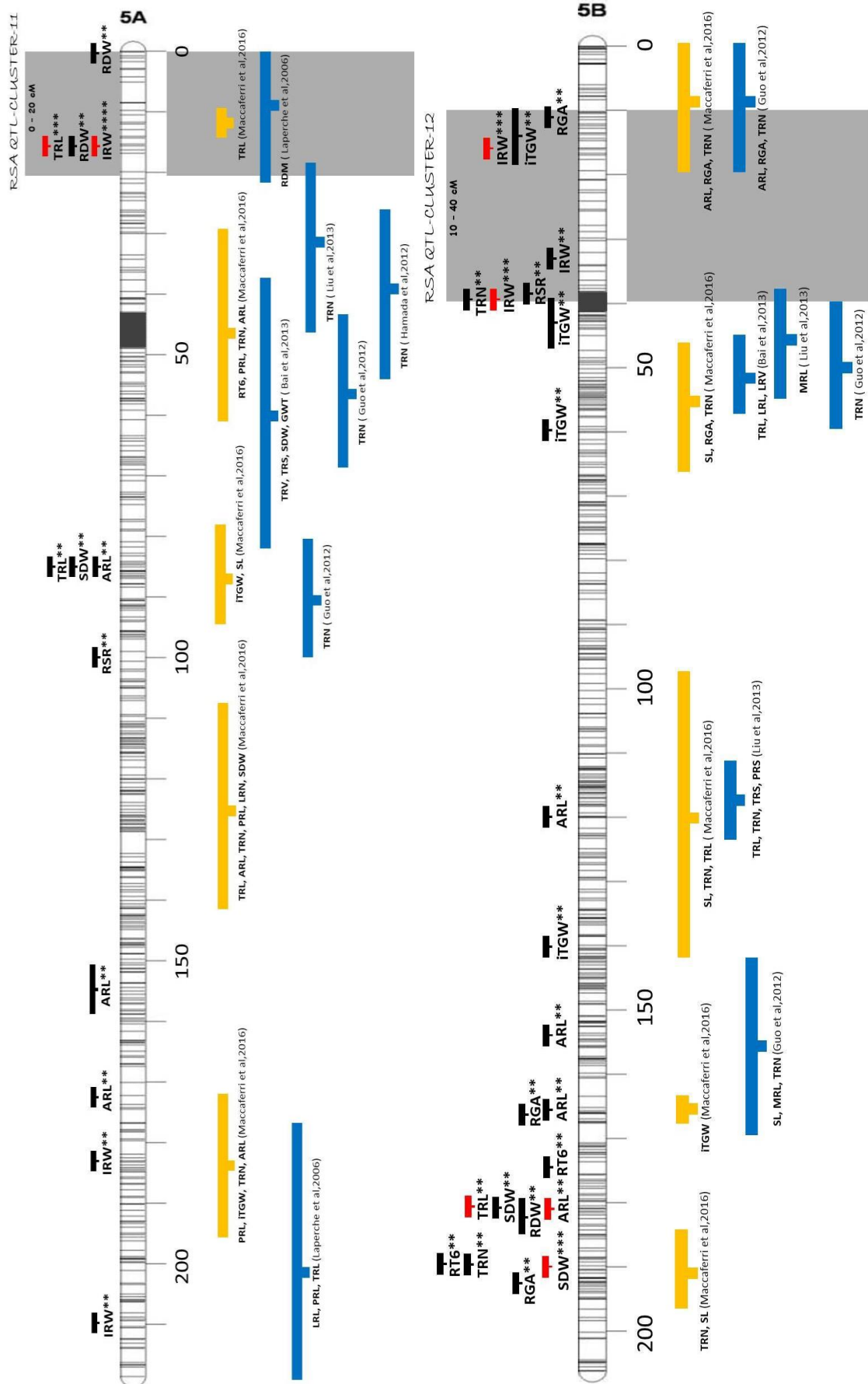
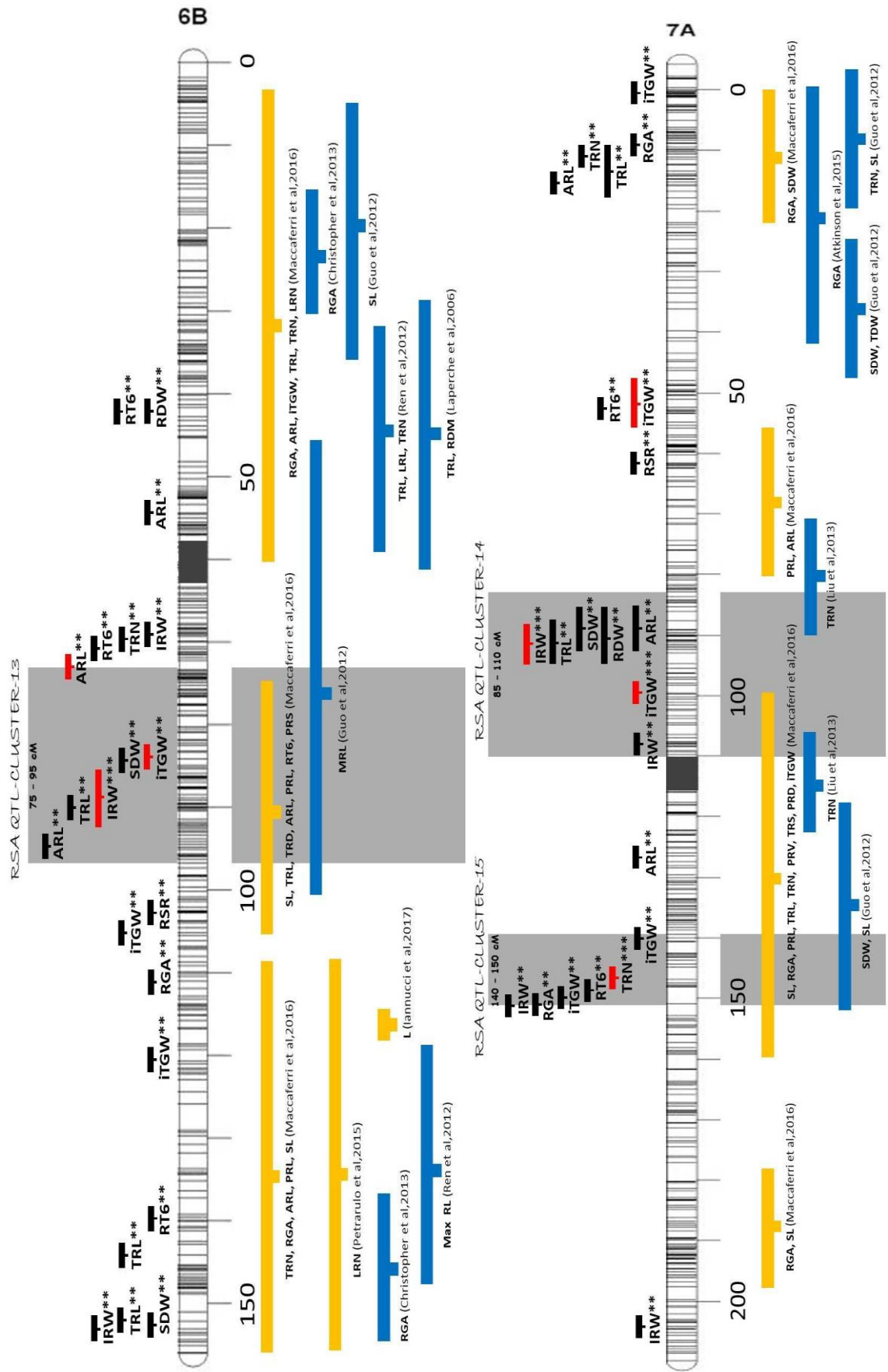


Figure 28. Genetic map of RSA QTLs identified in Ethiopian durum wheat accessions along with previously published studies projected onto SNP-based tetraploid consensus map published in Maccaferri *et al.* (2015). RSA QTLs identified in the present study are listed at the left side of the chromosomes bars; RSA QTLs identified in previous studies (orange-filled bars for durum wheat and blue-filled bars for bread wheat) listed at the right side. Grey-filled bands are for the major RSA QTL clusters and a special root growth angle (RGA) QTL clusters identified on chromosome 6AL from 105-125 cM.









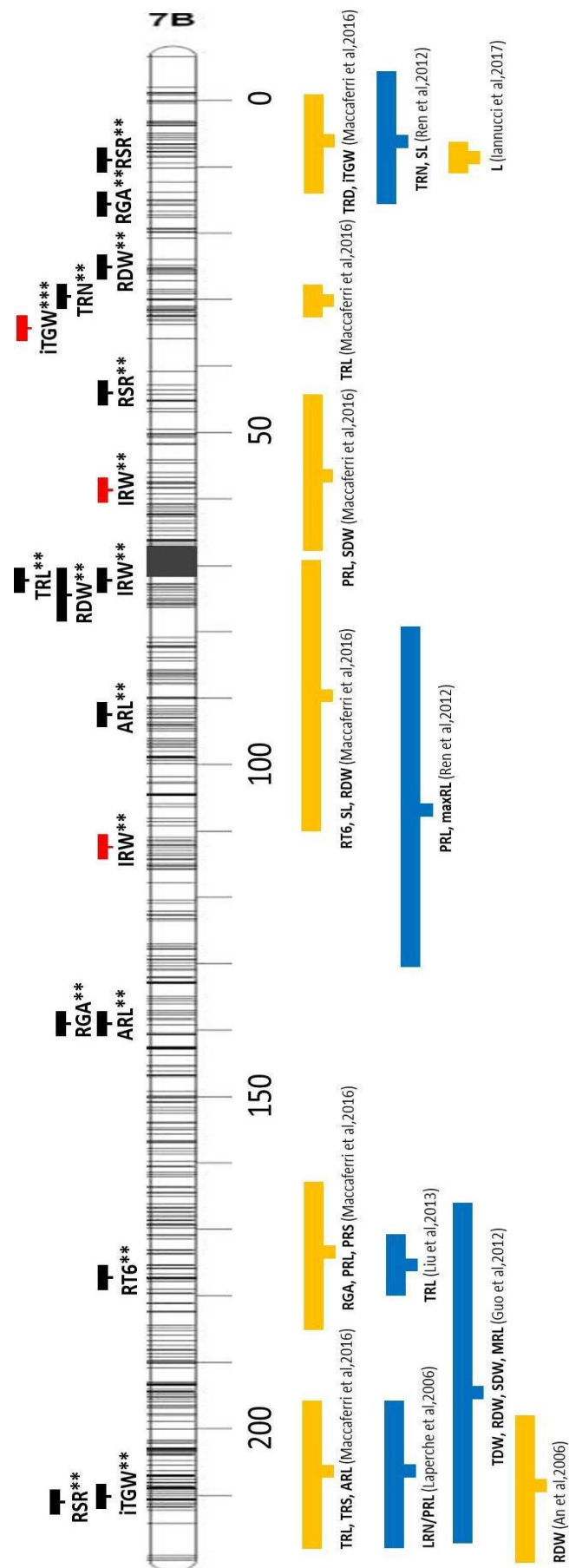


Figure 29. Genetic map of identified RSA QTLs in Ethiopian durum wheat and previously published studies in both bread and durum wheat projected onto SNP-based tetraploid consensus map published in Maccaferri *et al.* (2015).

RSA QTLs identified in the present study are listed at the left of chromosomes with their significance level (i.e. ** = marker-wise significance of P 0.01 (-LOGP=2); *** = marker-wise significance of P 0.001 (-LOGP=3) and ****, experiment-wise significance, P 0.05 (-LOGP=4)). Black bars are for QTLs with $r^2 < 5\%$; red bars for r^2 values in between 5 and 10 % and yellow bars for $r^2 > 10\%$. The length of bars indicates the confidence interval of each QTL/cluster of QTLs. The significance and color of bars indicated is for the QTL with higher values of significance and r^2 in the case of QTL clusters.

RSA QTLs from previously published studies in wheat have been projected on the consensus map and reported at the right side of chromosome bars as orange-filled for durum wheat and blue-filled for bread wheat. The length of the bars represents the confidence interval of single QTL/cluster of QTLs.

Major RSA QTL-clusters of the present study are stated as grey-banded intervals.

RSA acronyms used in the present study: TRL, total root length; ARL, average root length; RGA, root growth angle; TRN, total root number; RDW, root dry weight/experiment; IRW, individual root dry weight; SDW, shoot dry weight/experiment; RSR, root to shoot ratio; RT6, presence of the sixth root; iTGW, initial thousand grain weight.

Table 14.. Main RSA QTL clusters identified in Ethiopian durum wheat accessions and other studies.

QTL cluster	Chr	Interval (cM)	Main RSA trait			Other traits	Reference
			RSA trait	-logP	R ² (%)		
RSA QTL cluster-1	1A	5-25	TRN	3.3	5.7	RSR, RT6	Maccaferri <i>et al.</i> , 2016; Petrarulo <i>et al.</i> , 2015; Ren <i>et al.</i> , 2012
RSA QTL cluster-2	1A	120-140	SDW	3.3	6.3	RGA, IRW, TRL, RDW, ARL, RT6	Maccaferri <i>et al.</i> , 2016
RSA QTL cluster-3	1B	20-35	TRL	3.5	6.8	ARL, TRN, RT6, IRW, RDW, SDW,	Maccaferri <i>et al.</i> , 2016; Christopher <i>et al.</i> , 2013; Guo <i>et al.</i> , 2012; Kubo <i>et al.</i> , 2007; Liu <i>et al.</i> , 2013; Petrarulo <i>et al.</i> , 2015
RSA QTL cluster-4	2A	35.6	ARL	3.0	5.7	IRW, RDW, SDW, TRL	Maccaferri <i>et al.</i> , 2016
RSA QTL cluster-5	2B	160-185	IRW	3.5	6.7	RGA, RDW, RT6, SDW, TRL, ARL	Maccaferri <i>et al.</i> , 2016; Guo <i>et al.</i> , 2012
RSA QTL cluster-6	3A	70-100	RDW	3.2	5.8	TRN, IRW, SDW, RSR	Maccaferri <i>et al.</i> , 2016; Ren <i>et al.</i> , 2012
RSA QTL cluster-7	3B	40-65	SDW	3.1	5.9	TRL, RDW, IRW, RGA	Maccaferri <i>et al.</i> , 2016; Atkinson <i>et al.</i> , 2015; Liu <i>et al.</i> , 2013
RSA QTL cluster-8	3B	120-150	iTGW	4.2	8.7	TRN, RT6, RSR	Maccaferri <i>et al.</i> , 2016
RSA QTL cluster-9	4A	15-25	RDW	4.3	8.4	TRN, SDW, RT6	Maccaferri <i>et al.</i> , 2016
RSA QTL cluster-10	4B	80-115	TRN	3.6	6.9	RDW, RT6, SDW, IRW, TRL	Maccaferri <i>et al.</i> , 2016; Iannucci <i>et al.</i> , 2017; Liu <i>et al.</i> , 2013
RSA QTL cluster-11	5A	0-20	IRW	4.1	8.0	TRL, RSR, RDW	Maccaferri <i>et al.</i> , 2016; Laperche <i>et al.</i> , 2006
RSA QTL cluster-12	5B	10-40	IRW	3.2	5.9	iTGW, RSR, TRN, RGA	Maccaferri <i>et al.</i> , 2016; Guo <i>et al.</i> , 2012
*RGA QTL cluster	6A	105-125	RGA	6.9	16.1		Maccaferri <i>et al.</i> , 2016
RSA QTL cluster-13	6B	75-95	IRW	3.3	6.3	ARL, iTGW, SDW, TRL	Maccaferri <i>et al.</i> , 2016; Guo <i>et al.</i> , 2012
RSA QTL cluster-14	7A	85-110	iTGW	3.4	6.7	ARL, RDW, SDW, TRL, IRW	Maccaferri <i>et al.</i> , 2016; Liu <i>et al.</i> , 2013
RSA QTL cluster-15	7A	140-150	TRN	3.07	5.7	iTGW, RT6, IRW, RGA	Maccaferri <i>et al.</i> , 2016; Guo <i>et al.</i> , 2012

*A special RGA QTL clusters identified at chromosome 6A

5.3. Genome-Wide Association Mapping for Grain Shape and Color Related Traits

Understanding the genetic basis of complex quantitative traits of economic importance is a major tactic behind the whole progress in plant breeding. Genome-wide associations mapping (GWAS) is a strong statistical tool that comprises genotyping a large collection of accessions with tens of thousands of SNPs throughout the whole genome and conduct association analysis with phenotypic trait(s) of interest with the aim of dissecting the genetic bases of complex quantitative traits. For the last couples of decades, novel SNP marker genotyping platforms have brought the reality of genomic assisted selection through detection of quantitative trait loci (Tuberosa and Pozniak, 2014). The 90K wheat SNP array by Illumina allowed for precise genome wide scans that enable a highly accurate comparative analysis and QTL cross-referencing (Wang *et al.*, 2014; Maccaferri *et al.*, 2015). In the present study, 192 Ethiopian durum wheat accessions (167 landraces and 25 varieties) were used to conduct a GWAS analysis for grain weight, shape and color related traits. A significant variation was observed between the mean values of Ethiopian durum wheat accessions for all included traits that assured GWAS could be a powerful strategy to dissect QTLs for these valuable traits across the genomes.

Because of non-random mating, isolation or artificial selection, structured populations exist more or less in any plant population. Consequently, genetic loci could be spuriously associated with a trait when there is no real association. The probability of a false positive/Type I error increases in association mapping studies if the population structure is not appropriately accounted for (Pritchard *et al.*, 2000; Flint-Garcia *et al.*,

2003; Gupta *et al.* 2005; Yu *et al.*, 2006; Maccaferri *et al.*, 2011; Letta *et al.*, 2013). Hence, assessment of population structure is crucial prior to any GWAS analysis. The present panel was stratified into three distinct sub-groups. Sub-group two comprised varieties while landraces were sub-grouped into the other two sub-groups irrespective of their geographic origin. This admixture could arise because of the presence of higher seed exchanges rate between local farmers in local markets throughout the country.

Understanding the linkage disequilibrium (LD) pattern in a particular germplasm is essential for different reasons including: to select the marker density required for GWAS analysis; for experimental design needed to perform GWAS analysis, and for defining identified QTL regions (Siol *et al.*, 2017). Linkage disequilibrium (LD) analysis of the current panel was conducted using 10,789 polymorphic SNPs generated from the 90,000 wheat SNP chip by Illumina. The result indicated that the panel decays to the threshold of $r^2 = 0.3$ (the generally accepted limit to detect significant association with a QTL) at 2.25 cM.

In the present study, both GW and GL showed a significant correlation with L* and b*, while negative correlation with a*. As to our knowledge, there wasn't any published study yet that reports on the relationship between grain shape and color related traits in wheat. CIE b* (yellowness) showed a significant negative correlation with a* (redness) which is consistent with previous reports (Humphries *et al.*, 2004; Zhang *et al.*, 2009; Tsilo *et al.*, 2011; Zhai *et al.*, 2016; 2018; Goriewa-Duba *et al.*, 2018) but showed a significant positive correlation with L* (brightness). Goriewa-Duba *et al.* (2018) on the other hand, reported a highly significant positive correlation

between b^* and L^* . This difference might be due to the samples taken for analysis in which, unlike the present study, these reports were dependent on the flour (endosperm) part. For instance, Humphries *et al.* (2004) scored higher values of a^* and b^* but less L^* in the wheat bran than the flour. However, they reflected the presence of a significant correlation with the values of the color-related traits in the grain and flour across genotypes and concluded color values could be extrapolated from the easily accessible part of the grain. Some studies also reported the presence of strong positive correlation between b^* and a^* (Li *et al.*, 2011; Zhao *et al.*, 2013). CIE b^* has been used as an alternative measurement means for yellow pigment content (YPC), since they have a proven strong correlation (Roncallo *et al.*, 2012), which is an essential quality parameter in pasta industry. Red colored wheat grains on the other hand have been identified as resistant for pre-harvest sprouting and this relationship could be due either to the pleiotropic effect of genes controlling red-testa pigmentation (R) or to linkage between these genes and other genes affecting pre-harvest sprouting (Groos *et al.*, 2002).

Grain shape and color have an enormous importance for different reasons. Therefore, identifying QTLs for these traits are essential to foster transfer of favorable alleles based on selection strategies and breeding objectives. Grain shape and color related traits are crucial quality parameters with various uses and have been used as essential selection criteria in durum wheat breeding. Previous studies reported various QTLs across all chromosomes and genomes for grain length, grain width and color related traits using various populations. In the present study, the majority of QTL areas spotted for GL and GW were independent except in a single case on chromosome arm 5AL that is consistent with previous reports (Gegas *et al.*, 2010; Russo *et al.*, 2014;

Kumar *et al.*, 2016). In the present study, QTLs for considered traits were detected on similar chromosome regions with various studies reported previously. In consistency to this study, Chen *et al.* (2016) reported QTLs for GL on chromosome arms 1BS and 5AL and for GW on 4BS, 7BS and 7BL. Gao *et al.* (Gao *et al.*, 2015) identified a stable TGW QTL, QTKW.caas-7AL, across all the surveyed environments using an F8 recombinant inbred lines population of Chinese spring wheat. Ma *et al.* (2015) identified TaCYP78A3 gene of CYP78A family, encoding cytochrome CYP78A3 P450, on short arms of bread wheat chromosome group 7 (7AS, 7BS and 7DS) which was related with grain size and shape and silencing of this gene caused a notable decrement on these traits. Yan *et al.* (2019) detected TaGW8 gene, with TaGW8-B1a and TaGW8-B1b alleles, on chromosome 7B that had a significant effect on grain shape traits. Wang *et al.* (2015) cloned TaGS5 gene found on chromosomes 3AS and 3DS of Chinese bread wheat that controls thousand grain weight and grain width. In consistency with these reports, QTLs were detected for GL and GW on the same regions of chromosomes 7A and 7B in this study. Moreover, QTLs for grain shape traits were spotted in all chromosomes except 3A that are closer to previous studies (Ramya *et al.*, 2010; Russo *et al.*, 2014; Wu *et al.*, 2015; Chen *et al.*, 2016; Su *et al.*, 2018).

Many QTLs were previously identified for color related traits in both bread and durum wheat using various populations across all chromosomes (Mares and Campbell, 2001; Kuchel *et al.*, 2006; Sherman *et al.*, 2008; Zhang *et al.*, 2009; Li *et al.*, 2011; Tsilo *et al.*, 2011; Roncallo *et al.*, 2012; Zhao *et al.*, 2013; Zhai *et al.*, 2016, 2018). Previous studies showed that the Psy1 gene, a gene coding for the enzyme phytoene synthase 1 (Psy1) which is considered the rate-limiting step of carotenoid

biosynthetic pathway, co-segregates with yellow pigment content (YPC) and CIE b* at chromosomes 7BL (Pozniak *et al.*, 2007; Zhang and Dubcovsky, 2008) and 7AL (He *et al.*, 2008; Singh *et al.*, 2009). A second Psy functional gene (*Psy2*) was located on group 5 chromosomes of durum wheat (Pozniak *et al.*, 2007; Blanco *et al.*, 2009). Crawford and Francki (2013) identified single nucleotide polymorphism in the gene encoding lycopene-ecylcase that controls phenotypic variation for flour b* color on chromosome 3A. In agreement with these reports, in the present study, QTLs were detected for b* on the same chromosome arms 3AL, 5AS and 7BL. Additional b* QTLs were identified on chromosome arms 1BL, 2AL, 2BL, 4BS and 6AL. In this study, a major QTL controlling both L* (brightness) and a* (redness) at a single locus (IWB72154) were identified on the long arm of chromosome 2A. In addition, closer to this, another single locus (IWB8286) made a nominal QTL for L* (EPdwL*-2A.1) with negative effect and suggestive QTL for a* with positive effect. Since having positive effect for a* and negative effect for L*, this QTL could be a putative locus with two alleles. Sherman *et al.* (2008) identified a locus on chromosome group 3 in bread wheat for grain color with red as dominant and white as recessive alleles and explained as the degree of red color is additive, with genotypes homozygous dominant at all three loci (*R-A1b*, *R-B1b*, and *R-D1b*) having the darkest red color, and only those homozygous recessive at all three genes being white (*R-A1a*, *R-B1a*, and *R-D1a*). Moreover, 7 QTLs were identified for L* on chromosome arms 1AS, 2AS, 5AL, 6AL, 7AL (2) and 7BL and 4 QTLs for a* on chromosome arms 1AS, 2AL, 5AS, and 7AL. Most of QTLs spotted in the present study were closer to previous studies. For instance, Zahi *et al.* (2016) identified a major QTL for a* (*QFa.caas-2AL.2*) at the long arm of chromosome 2A and for b* (*QFb.caas-1BL.2*) at the long arm of chromosome 1B and *QFb.caas-5AS.1* at the short arm of

chromosome 5A that are closer to EPdwa*-2A, EPdwb*-1B and EPdwb*-5A detected in the current study, respectively.

Similar to the significant correlation observed between grain shape and color related traits in the phenotypic data, pleiotropic effect/tight linkage was observed in the MTA analysis between these traits. Five GW QTLs were spotted having a pleiotropic effect/tight linkage with color related traits on chromosome arms 2AL (two), 4BS, 5AL and 7BL. A single GL QTL was also identified having a pleiotropic effect/tight linkage with b* and a* on chromosome arm 5AS. There was no previous study which compiles both grain shape traits with color related traits for QTL analysis in wheat. Therefore, the nature of this effect spotted in the present study needs further investigation to have detailed clue of their genetic architecture.

6. CONCLUSION AND RECOMMENDATIONS

In this study, 192 Ethiopian durum wheat accessions comprising 167 landraces and 25 improved varieties were assembled and genotyped with a high density 90K wheat SNP array to analyze the linkage disequilibrium, population structure and genetic diversity of the panel and to spot QTLs for root system architecture and quality related traits via GWAS analysis.

The result unveiled the presence of higher genetic diversity in Ethiopian durum wheat that could enhance durum-breeding effort and promote sustainable conservation of the germplasm. Wheat is an important food security crop that plays key roles in maintaining peace and stability at global level. However, there is a huge gap between demand and supply especially in the Central and West Asia and North Africa (CWANA) and Sub-Saharan Africa (SSA) regions.

Highly significant phenotypic variation was recorded for all RSA traits in this study. Four major and thirty-four nominal RSA QTLs, of which 14 are novel, were identified across all chromosomes in Ethiopian durum wheat. Assimilating the root QTLs from the present and previously published studies could be an invaluable means to spot precise chromosome regions that have an effect on RSA traits. Evidence for significant QTL effects across different genetic materials is basic to pick QTL and apply MAS for enhancing crop production (Collins *et al.*, 2008; Tuberosa, 2012). In this regard, the majority of RSA QTLs identified in this study overlaps with previously reported RSA QTLs. Higher numbers of RSA QTLs were spotted on chromosome 4B particularly for root vigor traits (root length, number and weight) which is in agreement with Maccafarri *et al.* (2016). A cluster of RGA QTL is

identified on the long arm of chromosome 6A and *EPdwRGA-6A*, a major RGA QTL with higher phenotypic effect and reported by Maccafarri *et al.* (2016) as *QRga.ubo-6A.2*, is within the cluster.

Even though, reasonable genotypic and phenotypic data were employed in the current GWAS analysis for grain shape and color related traits, more environment and year phenotypic data could facilitate discovery of more putative QTLs across environments. Nonetheless, a strong novel QTL was identified from this study. For instance, a major QTL for redness and brightness traits has been detected on chromosome arm 2AL. Pleiotropic QTLs with an effect for both grain shape and color traits were spotted. The non-invasive, economically feasible digital image analysis could be a wise alternative to detect QTLs for these traits.

Based on the findings of the current study, the following recommendations are forwarded:

- ❖ In agreement with previous reports, the current study proved the presence of rich genetic variation in Ethiopian durum wheat that deserves sustainable utilization and conservation.
- ❖ Emphasis on the existing rich genetic variation for root system architectural traits in Ethiopian durum wheat should be given to exploit more based on suitable soil with water and nutrient conditions in Ethiopia.
- ❖ Validation of RSA-QTLs identified with higher significant MTA and phenotypic effect is highly recommended to deploy RSA through MAS for enhanced durum productivity.
- ❖ Validation and fine mapping of the major RGA-QTLs, *EPdwRGA-6A*, is highly recommended for further employment of RGA through MAS.

- ❖ Further investigation and validation of the major grain color QTL with a pleotropic effect for red and brightness identified on chromosome 2AL is recommended.
- ❖ Even though, major and novel QTLs were detected for grain shape and color-related traits in the current study, further GWAS studies with environment and year phenotypic data is highly recommended to explore more and to get precise and stable QTLs in Ethiopian durum wheat.

REFERENCES

- Abdallah, J.M., Goffinet, B., Cierco-Ayrolles, C. and Pérez Enciso, M. (2003). Linkage disequilibrium fine mapping of quantitative trait loci: A simulation study. *Genet Sel Evol* 35:513–532.
- Abdurakhmonov, I.Y. and Abdukarimov, A. (2008). Application of association mapping to understanding the genetic diversity of plant germplasm resources. *Int J Plant Genomics* 574–927.
- Able, J. and Atienza, S. (2014). Durum wheat for the future: challenges, research and prospects in the 21st century. *Crop Pasture Sci.* 65:124
- Alamerew, S., Chebotar, S., Huang, X., Röder, M., and Börner, A. (2004). Genetic diversity in Ethiopian hexaploid and tetraploid wheat germplasm assessed by microsatellite markers. *Genet. Resour. Crop Evol.* 51:559–567.
- Ammar, K., Kronstad, W.E. and Morris, C.F. (2000). Bread-making quality of selected durum wheat genotypes and its relationship with high molecular weight glutenin subunits allelic variation and gluten protein polymeric composition. *Cereal Chem.* 77:230–236.
- Ammiraju, J. S., Dholakia, B. B., Santra, D. K., Singh, H., Lagu, M. D., Tamhankar, S. A., et al. (2001). Identification of inter simple sequence repeat (ISSR) markers associated with seed size in wheat. *Theor. Appl. Genet.* 102:726–732.
- Amri, A., Hatchett, J.H., Cox, T.S., Bouhassini, M.E. and Sears, R.G. (1990). Resistance to Hessian fly from North African durum wheat germplasm. *Crop Sci.* 30:378–381.
- Andreas, S. and Bryce, G. (2016). Concepts and relevance of genome-wide association studies. *Science Progress* 99(1):59–67.

- Andrew, R.(2016). FigTree: Tree figure drawing tool, Version 1.4.3. Institute of Evolutionary Biology. United Kingdom: University of Edinburgh.
- Angelovici, R., Lipka, A.E., Deason, N., Gonzalez–Jorge, S., Lin, H.N., Cepela, J., et al. (2013). Genome-wide analysis of branched-chain amino acid levels in *Arabidopsis* seeds. *Plant Cell* 25:4827–4843.
- Appleby, N., Edwards, D. and Batley, J. (2009). New technologies for ultrahigh throughput genotyping in plants. *Methods Mol Biol* 513:19–39.
- Arts, I.C. and Hollman, P.C.(2005). Polyphenols and disease risk in epidemiologic studies. *Am J Clin Nutr.* 81:317S–325S.
- Atkinson, J. A.,Wingen, L. U., Griffiths,M., Pound,M. P., Gaju, O., Foulkes,M. J., et al. (2015). Phenotyping pipeline reveals major seedling root growth QTL in hexaploid wheat. *J. Exp. Bot.* 66:2283–2292.
- Atwell, S., Li Y.S., Vilhjalmsen, B.J., Willems, G., Horton, M., Li, Y., et al. (2010). Genome-wide association study of 107 traits in *Arabidopsis thaliana* inbred lines. *Nature* 465:627–63.
- Badebo, A., Gelalcha, S., Ammar, K., Nachit, M., Abdalla, O. and McIntosh, R. (2009). “Overview of durum wheat research in Ethiopia: challenges and prospects,” in Proceedings, Oral Papers and Posters, Technical Workshop, Borlaug Global Rust Initiative, Cd. Obregón, Sonora, Mexico, 17–20March, 2009, (Ciudad Obregón: Borlaug Global Rust Initiative), 143–149.
- Bai, C., Liang, Y., and Hawkesford, M. J. (2013). Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. *J. Exp. Bot.* 64:1745–1753.
- Barrett, J. C., Fry, B., Maller, J., and Daly, M. J. (2005). Haploview: analysis and visualization of LD and haplotype maps. *Bioinformatics* 21:263–265.

- Bechere, E., Belay, G., Mitiku, D. and Merker, A. (1996). Phenotypic diversity of tetraploid wheat landraces from northern and north-central regions of Ethiopia. *Hereditas* 124:165–172.
- Bekele, E. (1984). Analysis of regional patterns of phenotypic diversity in the Ethiopian tetraploid and hexaploid wheats. *Hereditas* 100:119–134.
- Ben-Abu, Y., Tzfadia, O., Maoz, Y., Kachanovski, D.E., Melamed-Bessu, C., Feldman, M. and Levy, A.A (2014). Durum wheat evolution: A genomic analysis. In: Porceddu E. (ed.), Damania A.B. (ed.), Quilset C.O. (ed.). *Proceedings of the International Symposium on Genetics and Breeding of Durum Wheat*. Bari CIHEAM 31–45.
- Bernardo, R. (2008). Molecular markers and selection for complex traits in plants: learning from the last 20 years. *Crop Science* 48(5):1649–1664.
- Biggeri, F., Federico, B. and Herrmann, R. (2018). Linking small-scale farmers to the durum wheat value chain in Ethiopia: Assessing the effects on production and wellbeing. *Food policy* 79:77-91.
- Blanco, A., Colasuonno, P., Gadaleta, A., Mangini, G., Schiavulli, A, Simeone, R., et al.. (2011). Quantitative trait loci for yellow pigment concentration and individual carotenoid compounds in durum wheat. *J Cereal Sci* 54:255–264.
- Blanco, A., Schiavulli, A., Colasuonno, P., Gadaleta, A., Sonnante, G. and Pignone, D. (2009). Mapping of phytoene synthase (psy2) genes on group 5 chromosomes of durum wheat. In: Proceedings of the 19th International Triticeae Mapping Initiative, Clermont-Ferrand, France; August 31–September 4
- Blum, A. (1988). Plant breeding for stress environments. Boca Raton, Florida: CRC Press.

- Blum, A. (2009). Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Res.* 112:119–123.
- Blum, A., Shipiler, L., Golan, G. and Mayer, J. (1989). Yield stability and canopy temperature of wheat genotypes under drought stress. *Field Crops Res.* 22:289–296.
- Borlaug, N. E. (1972). Breeding wheat for high yield, wide adaptation, and disease resistance. In International Rice Research Institute (Ed.), *Rice Breeding* (pp. 581e 592). Los Banos, Philippines: IRRI.
- Borrell, A.K., Mullet, J.E., George-Jaeggli, B., van Oosterom, E.J., Hammer, G.L., Klein, P.E., and Jordan, D.R. (2014). Drought adaptation of stay green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. *J. Exp. Bot.* 65:6251–6263.
- Bouchet, S., Servin, B., Bertin, P., Madur, D., Combes, V., Dumas, F., et al. (2013). Adaptation of maize to temperate climates: mid-density genome-wide association genetics and diversity patterns reveal key genomic regions, with a major contribution of the Vgt2 (ZCN8) locus. *PLoS ONE* 8(8):e71377.
- Bozzini, A., (1988). Origin, Distribution and Production of Durum Wheat in the World. In: *Durum Wheat: Chemistry and Technology*, Fabriani, G. and C. Lintas (Eds.). American Association of Cereal Chemists, St. Paul, MN. America, ISBN-13: 9780913250501, 1–16.
- Brachi, B., Faure, N., Bergelson, J., Cuguen, J. and Roux, F. (2013). Genome-wide association mapping of flowering time in *Arabidopsis thaliana* in nature: genetics for underlying components and reaction norms across two successive years. *Acta Bot Gallica* 160:205–218.

- Brachi, B., Faure, N., Horton, M., Flahauw, E., Vazquez, A., Nordborg, M., et al. (2010). Linkage and association mapping of *Arabidopsis thaliana* flowering time in nature. *PLoS Genetics* 6(5):e1000940.
- Bradbury PJ, Zhang Z, Kroon DE, Casstevens TM, Ramdoss Y, Buckler ES. (2007) TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics* 23:2633–2635.
- Breseghele, F., and Sorrells, M. E. (2006). Association mapping of kernel size and milling quality in wheat (*Triticum aestivum* L.) varieties. *Genetics* 172:1165–1177. doi: 10.1534/genetics.105.044586
- Browning, S. R. and Browning, B. L. (2007). Rapid and accurate haplotype phasing and missing data inference for whole genome association studies by use of localized haplotype clustering. *Am J Hum Genet* 81:1084–1097.
- Buckler, E.S., Holland, J.B., Bradbury, P.J., Acharya, C.B., Brown, P.J., Browne, C., et al. (2009). The genetic architecture of maize flowering time. *Science* 325:714–718.
- Burghardt, L.T., Young, N.D. and Tiffin, P. (2017). A guide to genome-wide association mapping in plants. *Curr. Protoc. Plant Biol.* 2:22–38.
- Burton, A.L., Williams, M., Lynch, J.P. and Brown, K.M. (2012). RootScan: Software for high throughput analysis of root anatomical traits. *Plant Soil* 357:189–203.
- Bush, W.S. and Moore, J.H. (2012). Chapter 11: Genome-wide association studies. *PLoS Comput. Biol.* 8(12):e1002822.
- Caldwell, K.S., Langridge, P. and Powell, W. (2004). Comparative sequence analysis of the region harboring the hardness locus in barley and its colinear region in rice. *Plant Physiol* 136:3177–3190.

- Caldwell, K.S., Russell, J., Langridge, P. and Powell, W. (2006). Extreme population-dependent linkage disequilibrium detected in an inbreeding plant species, *Hordeum vulgare*. *Genetics* 172:557–567.
- Campbell, B.T., Baenziger, P.S., Gill, K.S., Eskridge, K.M., Budak, H., Erayman, M., et al. (2003). Identification of QTLs and environmental interactions associated with agronomic traits on chromosome 3A of wheat. *Crop Sci* 43:1493–1505
- Campbell, K.G., Finney, P.L., Bergman, C.J., Gualberto, D.G., Anderson, J.A., Giroux, M.J., et al. (2001). Quantitative trait loci associated with milling and baking quality in a soft × hard wheat cross. *Crop Sci* 41:1275–1285.
- Camus-Kulandaivelu, L., Veyrieras, J.B., Gouesnard, B., Charcosset, A. and Manicacci, D. (2007). Evaluating the Reliability of Structure Outputs in Case of Relatedness between Individuals. *Crop Science* 47:887–892.
- Canè, M. A., Maccaferri, M., Nazemi, G., Salvi, S., Francia, R., Colalongo, C., et al. (2014). Association mapping for root architectural traits in durum wheat seedlings as related to agronomic performance. *Mol Breed.* 34:1629–1645.
- Cao, P., Ren, Y., Zhang, K., Teng, W., Zhao, X., Dong, Z., et al. (2014). Further genetic analysis of a major quantitative trait locus controlling root length and related traits in common wheat. *Mol. Breed.* 33, 975–985.
- Carlson, C.S., Eberle, M.A., Rieder, M.J., Yi, Q., Kruglyak, L. and Nickerson, D.A. (2004). Selecting a maximally informative set of single-nucleotide polymorphisms for association analyses using linkage disequilibrium. *The American Journal of Human Genetics* 74:106-120.
- Ceccarelli, S. and Grando, S. (1996). Drought as a challenge for the plant breeder. *J. Plant Growth Regul.* 20:149–155.

- Chen, C.D., Sloane, J.A., Li, H., Aytan, N., Giannaris, E.L., Zeldich, E., et al. (2013). The antiaging protein Klotho enhances oligodendrocyte maturation and myelination of the CNS. *J Neurosci.* 33(5):1927–39.
- Chen, G., Zhang H., Deng, Z., Wu, R., Li, D., Wang, M. and Tian. J (2016). Genome-wide association study for kernel weight-related traits using SNPs in a Chinese winter wheat population. *Euphytica* 212:173–185.
- Chen, H.D., Xie, W.B., He, H., Yu, H.H., Chen, W., Li, J., et al. (2014). A high-density SNP genotyping array for rice biology and molecular breeding. *Mol Plant* 7:541–553.
- Chen, Q.F., Yen, C. and Yang, J.L. (1998). Chromosome location of the gene for brittle rachis in the Tibetan weederace of common wheat. *Genet. Resour. Crop Evol.* 45:407–410.
- Ching, A., Caldwell, K.S., Jung, M., Dolan, M., Smith, O.S., Tingey, S., et al. (2002). SNP frequency, haplotype structure and linkage disequilibrium in elite maize inbred lines. *BMC Genet* 3:19.
- Christopher, J., Christopher, M., Jennings, R., Jones, S., Fletcher, S., Borrell, A., et al. (2013). QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water-limited environments. *Theor. Appl. Gen.* 126:1563–1574.
- CIE (1986). Publication 15.2. *Colorimetry*, 2nd ed.; CIE (Commission Internationale de l’Eclairage) Central Bureau Kegelgasse: Wien, Austria, 27-A-1030.
- Cockram, J., White, J., Zuluaga, D.L., Smith, D., Comadran, J., Macaulay, M., et al. (2010). Genome-wide association mapping to candidate polymorphism resolution in the unsequenced barley genome. *Proc Natl Acad Sci USA* 107(50):21611–21616.

- Colasuonno, P., Gadaleta, A., Giancaspro, A., Nigro, D., Giove, S., Incerti, O., et al. (2014). Development of a high-density SNP-based linkage map and detection of yellow pigment content QTLs in durum wheat. *Mol. Breed.* 34:1563–1578.
- Collard, B.C. and Mackill, D.J. (2008). Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philos Trans R Soc Lond B Biol Sci* 363(1491):557–72.
- Collins, N.C., Tardieu, F. and Tuberosa, R. (2008). Quantitative trait loci and crop performance under abiotic stress: where do we stand? *Plant Physiol.* 147:469–486.
- Collins, T.J. (2007). ImageJ for microscopy. *BioTechniques* 43:25–30
- Colomba, M.S. and Gregorini, A. (2011). Genetic diversity analysis of the durum wheat Graziella Ra, *Triticum turgidum* L. subsp. *durum* (Desf.) Husn. (Poales, Poaceae). *Biodivers. J.* 2:73–84.
- Crawford, A. C., and Francki, M. G. (2013). Lycopene-ε-cyclase (e- LCY3A) is functionally associated with QTL for flour b* color on chromosome 3A in wheat (*Triticum aestivum* L.). *Mol. Breed.* 31:737–741.
- CSA, (2013). *Agriculture: Statistical Abstracts*. Addis Ababa, Ethiopia, 2003–2012.
- Cuesta–Marcos, A., Szucs, P., Close, T.J., Filichkin, T., Muehlbauer, G.J., Smith, K.P. and Hayes, P.M. (2010). Genome-wide SNPs and re-sequencing of growth habit and inflorescence genes in barley: implications for association mapping in germplasm arrays varying in size and structure. *BMC Genomics* 11:107.
- Cui, F., Ding, A.M., Li, J., Zhao, C.H., Li, X.F., Feng, D.S., et al. (2011). Wheat kernel dimensions: How do they contribute to kernel weight at an individual QTL? *J. Genet.* 90:409–425.

- de Dorlodot, S., Forster, B., Pages, L., Price, A., Tuberosa, R. and Draye, X. (2007). Root system architecture: opportunities and constraints for genetic improvement of crops. *Trends Plant Sci.* 12:474–481.
- De Vita, P., Riefolo, C., Codianni, P., Cattivelli, L. and Fares, C. (2006). Agronomic and qualitative traits of *T. turgidum* ssp. *dicoccum* genotypes cultivated in Italy. *Euphytica* 150:195–205.
- Dholakia, B.B., Ammiraju, J.S., Singh, H., Lagu, M.D., Roder, M.S., Rao, V.S., et al. (2003). Molecular marker analysis of kernel size and shape in bread wheat. *Plant Breed* 122:392–395
- Dubčovský, j. and Dvořák, j. (2007). Genome plasticity a key factor in the success of polyploid wheat under domestication. *Science* 316:1862–1866.
- Dwyer, J.H., Navab, M., Dwyer, K.M., Hassan, K., Sun, P., Shircore, A., et al. (2001). Oxygenated carotenoid lutein and progression of early atherosclerosis: The Los Angeles Atherosclerosis Study. *Circulation* 103:2922–2927.
- Dziki, D. and Laskowski, J. (2005). Wheat kernel physical properties and milling process. *Acta Agrophys* 6:59–71.
- Elouafi, I., Nachit, M.M. and Martin, L.M. (2001). Identification of a microsatellite on chromosome 7B showing a strong linkage with yellow pigment in durum wheat (*Triticum turgidum* L. var. durum). *Hereditas* 135:255–261.
- Elshire, R.J., Glaubitz, J.C., Sun, Q., Poland, J.A., Kawamoto, K., Buckler, E.S. and Mitchell, S.E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE* 6(5):e19379.
- Eltaher, S., Sallam, A., Belamkar, V., Emara, H.A., Nower, A.A., Salem, K.F.M., Poland, J. and Baenziger, P.S. (2018). Genetic Diversity and Population Structure

- of F3:6 Nebraska Winter Wheat Genotypes Using Genotyping-By-Sequencing. *Front. Genet.* 9:76.
- Ersoz, E., Yu, J. and Buckler, E. (2009). Applications of Linkage Disequilibrium and Association Mapping in Maize. A.L. Kriz, B.A. Larkins (eds.), *Molecular Genetic Approaches to Maize Improvement* 173. *Biotechnology in Agriculture and Forestry, Springer* 63:173–195.
- Eticha, F., Bekele, E., Belay, G., Börner, A. (2005). Phenotypic diversity in tetraploid wheats collected from Bale and Wello regions of Ethiopia. *Plant Genet. Resour.* 3:35–43.
- Evanno, G., Regnaut, S. and Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol. Ecol.* 14:2611–2620.
- Evenson, R.E. and Gollin, D. (2003). Assessing the Impact of the Green Revolution, 1960 to 2000. *Science* 300:758–762.
- Evers, A. D. and Withey, R. P. (1989). Use of image analysis to predict milling extraction rates of wheats. *Food Microstruct.* 8:191–199.
- Excoffier, L. and Lischer, H.E. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and windows. *Mol Ecol Resour.* 10:564–567.
- Famoso, A.N., Zhao, K., Clark, R.T., Tung, C.W., Wright, M.H., Bustamante, C., et al. (2011). Genetic architecture of aluminum tolerance in rice (*Oryza sativa*) determined through genome-wide association analysis and QTL mapping. *PLoS Genet* 7(8):e1002221.
- FAO (Food and Agriculture Organization) (2015). *Agricultural Production Statistics*. FAOSTAT. Rome.

- Feldman, M. (2001). The origin of cultivated wheat. In: *The World Wheat Book*. Bonjean A., Angus W. (eds). Lavoisier Tech. & Doc., Paris, pp. 3–56.
- Feldman, M. and Kisslev, M.E. (2007). Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. *Israel J. Plant Sci.* 55:207–221.
- Ficco, D.B.M., Mastrangelo, A.M., Trono, D., Borrelli, G.M., De Vita, P., Fares, C., et al. (2014). The colors of durum wheat: a review. *Crop & Pasture Science* 65:1–15.
- Fleury, D., Jefferies, S., Kuchel, H. and Langridge, P. (2010). Genetic and genomic tools to improve drought tolerance in wheat. *J. Exp. Bot.* 61:3211–3222.
- Flint–Garcia, S.A., Thornsberry, J.M. and Buckler, E.S. (2003). Structure of linkage disequilibrium in plants. *Annual Review of Plant Biology* 54:357–374.
- Friebe, B. and Gill, B.S. (1996). Chromosome bandings and genome analysis in diploid and cultivated polyploid wheats. In: *Methods of Genome Analysis in plants*, Jahuar P.P. (ed.) CRC Press, pp. 39–60.
- Furbank, R. T. and Tester, M. (2011). Phenomics–technologies to relieve the phenotyping bottleneck. *Trends Plant Sci.* 16:635–644.
- GAIN (2018). Global Agricultural Information Network Report: Ethiopia 1813, Addis Ababa: USDA.
- Galeano, C.H., Cortes, A.J., Fernandez, A.C., Soler, A., Franco–Herrera, N., Makunde, G., et al. (2012). Gene–based single nucleotide polymorphism markers for genetic and association mapping in common bean. *BMC Genet* 13:48.
- Ganal, M. W. and Röder, M. S. (2007). Microsatellite and SNP markers in wheat breeding. In: R.K. Varshney and R. Tuberosa (Eds.) *Genomics Assisted Crop Improvement: Genomics Applications in Crops* (Vol. 2), pp.1–24 (Springer), Netherlands, Dordrecht.

- Ganal, M.W., Durstewitz, G., Polley, A., Berard, A. Buckler, E.S., Clarke, J.D., et al. (2011). A large maize (*Zea mays* L.) SNP genotyping array: development and germplasm genotyping, and genetic mapping to compare with the B73 reference genome. *PLoS ONE* 6(12):e28334.
- Gao, F., Wen, W., Liu, J., Rasheed, A., Yin, G., Xia, X., et al. (2015). Genome-Wide Linkage Mapping of QTL for Yield Components, Plant Height and Yield-Related Physiological Traits in the Chinese Wheat Cross Zhou 8425B/Chinese Spring. *Front Plant Sci.* 6:1099.
- Gegas, V.C., Nazari, A., Griffiths, S., Simmonds, J., Fish, L., Orford, S., et al. (2010). A genetic framework for grain size and shape variation in wheat. *Plant Cell* 22:1046–1056.
- Gifford, M.L., Banta, J.A., Katari, M.S., Hulsmans, J., Chen, L., Ristova, D., et al. (2013). Plasticity regulators modulate specific root traits in discrete nitrogen environments. *PLoS Genet* 9(9):e1003760
- Giura, A. and Saulescu, N. N. (1996). Chromosomal location of genes controlling grain size in a large grained selection of wheat (*Triticum aestivum* L.). *Euphytica* 89:77–80.
- Goncharov, N.P. (2011). Genus *Triticum* L. taxonomy: the present and the future *Plant Syst. Evol.* 295:1–11.
- Gorfu, A., Girma, B. and Girma, K. (2001). Present status and future direction of wheat research and development in Ethiopia. In: Wall, P. C. (ed.). *Wheat and Weeds: Food and Feed Proceedings of Two Stakeholder Workshops*. Ethiopian Agricultural Research Organization, Addis Ababa, Ethiopia, pp.167–206.

- Goriewa-Duba, K., Duba, A., Wachowska, U. and Wiwart, M. (2018). An Evaluation of the Variation in the Morphometric Parameters of Grain of Six *Triticum* Species with the Use of Digital Image Analysis. *Agronomy* 8:296.
- Green, J.M., Appel, H., Rehrig, E.M., Harnsomburana, J., Chang, J-F., Balint-Kurti, P. and Shyu, C-R. (2012). PhenoPhyte: a flexible affordable method to quantify 2D phenotypes from imagery. *Plant Methods* 8:45.
- Gregory, P.J., Bengough, A.G., Grinev, D., Schmidt, S., Thomas, W.T.B., Wojciechowski, T. and Young, I.M. (2009). Root phenomics of crops: opportunities and challenges. *Funct. Plant Biol.* 36:922–929.
- Groos, C., Gay, G., Perretant, M.R., Gervais, L., Bernard, M., Dedryver, F. and Charmet, G. (2002). Study of the relationship between pre-harvest sprouting and grain color by quantitative trait loci analysis in a white × red grain bread-wheat cross. *Theor Appl Genet* 104:39–47.
- Guo, Y., Kong, F., Xu, Y., Zhao, Y., Liang, X., Wang, Y., An, D., and Li, S. (2012). QTL mapping for seedling traits in wheat grown under varying concentrations of N, P and K nutrients. *Theor Appl Genet.* 124:851–865.
- Gurung, S., Mamidi, S., Bonman, J.M., Xiong, M., Brown-Guedira, G. and Adhikari, T.B. (2014). Genome-Wide Association Study Reveals Novel Quantitative Trait Loci Associated with Resistance to Multiple Leaf Spot Diseases of Spring Wheat. *PLoS ONE* 9(9):e108179.
- Habash, D.Z., Kehel, Z. and Nachit, M. (2009). Genomic approaches for designing durum wheat ready for climate change with a focus on drought. *J. Exp. Bot.* 60:2805–2815.
- Haile, J.K., Hammer, K., Badebo, A., Nachit, M.M. and Röder, M. S. (2013). Genetic diversity assessment of Ethiopian tetraploid wheat landraces and improved durum

- wheat varieties using microsatellites and markers linked with stem rust resistance. *Genet. Resour. Crop Evol.* 60:513–527. doi: 10.1007/s10722-012-9855-1
- Hailu, G-M. (1991). Wheat productions and research in Ethiopia. In: Wheat Research in Ethiopia: A Historical Perspective. Gebre-Mariam, H., Tanner, D.G. & Huluka, M. (eds), IAR/CIMMYT, pp. 1-15. Addis Ababa, Ethiopia.
- Hamada, A., Nitta, M., Nasuda, S., Kato, K., Fujita, M., Matsunaka, H., et al. (2012). Novel QTLs for growth angle of seminal roots in wheat (*Triticum aestivum* L.). *Plant Soil* 354, 395–405.
- Hamblin, M.T., Fernandez, S. Casa, M.G., Mitchell, A.M. Paterson, S.E., and Kresovich, S. (2005). Equilibrium processes cannot explain high levels of short– and medium–range linkage disequilibrium in the domesticated grass *Sorghum bicolor*. *Genetics* 171(3):1247–1256.
- Hammer, K., Filatenko, A.A. and Pistrick, K., (2011). Taxonomic remarks on *Triticum* L. and *Triticosecale* Wittm. *Genet. Resour. Crop Evol.* 58:3–10.
- Han, B. and Huang, X. (2013). Sequencing-based genome-wide association study in rice. *Curr. Opin. Plant Biol* 16:133–138.
- Hao, Z.F., Li, X.H., Xie, C.X., Weng, J.F., Li, M.S., Zhang, D.G., et al. (2011). Identification of functional genetic variations underlying drought tolerance in maize using SNP markers. *J Integr Plant Biol* 53:641–652.
- Harlan, J. (1996). Ethiopia: A centre of diversity. *Econo Bot.* 23:124–32.
- Hawkes, J. G., Maxted, N. and Ford-Lloyd, B. V. (2000). The ex situ Conservation of Plant Genetic Resources, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hawkesford, M.J. (2014). Reducing the reliance on nitrogen fertilizer for wheat production. *J Cereal Sci.* 59:276–283. doi: 10.1016/j.jcs.2013.12.001

- Hayes, B. (2013). Overview of Statistical Methods for Genome–Wide Association Studies (GWAS). On: Cedric, G., Julius, V. and Hayes, B. (eds.) *Genome–Wide Association Studies and Genomic Prediction: Methods in Molecular Biology*. Springer Science + Business, human press. 1019:149–169.
- Heng, Y., Manish R., Babu, V., Lijuan, Z., Pengyin, C., Rajeev, K. V., and Henry, T. N. (2018). Genetic diversity of root system architecture in response to drought stress in grain legumes. *J. Exp. Bot.* 69:3267–3277. doi: 10.1093/jxb/ery082
- Hill, W.G. and Weir, B.S. (1988). Variances and covariances of squared linkage disequilibria in finite populations. *Theor Popul Biol* 33:54–78.
- Hinds, T.S., West, W.L. and Knight, E.M. (1997). Carotenoids and retinoids-a review of research, clinical, and public health applications. *Journal of Clinical Pharmacology* 37:551–558.
- Hirschhorn, J. N., and Daly, M. J. (2005). Genome-wide association studies for common diseases and complex traits. *Nat. Rev. Genet.* 6: 95–108.
- Hoggart, C.J., Whittaker, J.C., De Iorio, M., and Balding, D.J. (2008). Simultaneous Analysis of All SNPs in Genome-Wide and Re-Sequencing Association Studies. *PLoS Genet* 4(7):e1000130.
- Houle, D., Govindaraju, D. R. and Omholt, S. (2010). Phenomics: the next challenge. *Nat. Rev. Genet.* 11:855–866.
- Huang, J., Zhang, J.H., Li, W.Z., Hu, W., Duan, L.C., Feng, Y., et al. (2013). Genome-wide association analysis of ten chilling tolerance indices at the germination and seedling stages in maize. *J Integr Plant Biol* 55:735–744.
- Huang, X., Feng, Q., Qian, Q., Zhao, Q., Wang, L, Wang, A., et al. (2009). High-throughput genotyping by whole–genome re–sequencing. *Genome Res.*19:1068–76.

- Huang, X., Wei, X., Sang, T., Zhao, Q., Feng, Q., Zhao, Y., et al. (2010). Genome-wide association studies of 14 agronomic traits in rice landraces. *Nat. Genet.* 42:961–67.
- Huang, X.H., Zhao, Y., Wei, X.H., Li, C.Y., Wang, A., Zhao, Q. et al. (2012). Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. *Nat Genet* 44:32–39.
- Humphries, J.M., Graham, R.D. and Mares, D.J. (2004). Application of reflectance color measurement to the estimation of carotene and lutein content in wheat and triticale. *Journal of Cereal Science* 40:151–159.
- Hung, H.Y., Shannon, L.M., Tian, F., Bradbury, P.J., Chen, C., FlintGarcia, S.A., et al. (2012). ZmCCT and the genetic basis of day-length adaptation underlying the post domestication spread of maize. *Proc Natl Acad Sci U S A* 109:E1913–E1921.
- Hwang, E.Y., Song, Q.J., Jia, G.F., Specht, J.E., Hyten, D.L., Costa, J., Cregan, P.B. (2014). A genome-wide association study of seed protein and oil content in soybean. *BMC Genomics* 15:1.
- Iannucci, A., Marone, D., Russo, M. A., De Vita, P., Miullo, V., Ferragonio, P., et al. (2017). Mapping QTL for root and shoot morphological traits in a Durum Wheat $\times$ *T. dicoccum* segregating population at seedling stage. *Int. J. Genomics* 2017:6876393. Doi: <https://doi.org/10.1155/2017/6876393>
- IBC (2008). Ethiopia: Second Country Report on the State of PGRFA to FAO. Addis Ababa, Ethiopia. Available at <http://www.pgrfa.org>
- Iwata, H. and Ukai, Y. (2002). SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptic fourier descriptors. *J Hered* 93:384–385.
- Jain, S.K. (2000). Human aspects of plant biodiversity. *Economic Botony* 54:459–470.

- Jauhar, P.P. and Peterson, T.S. (2013). Synthesis and Characterization of Advanced Durum Wheat Hybrids and Addition Lines with *Thinopyrum* Chromosomes. *Journal of Heredity* 104(3):428–436.
- Jombart, T., Devillard, S. and Balloux, F. (2010). Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* 11:94.
- Kabbaj, H., Sall, A.T., Al-Abdallat, A., Geleta, M., Amri, A., Filali-Maltouf, A., et al. (2017). Genetic Diversity within a Global Panel of Durum Wheat (*Triticum durum*) Landraces and Modern Germplasm Reveals the History of Alleles Exchange. *Front. Plant Sci.* 8:1277. doi: 10.3389/fpls.2017.01277
- Kabir, M.R., Liu, G., Guan, P.F., Wang, F., Khan, A.A., Ni, Z.F., et al. (2015). Mapping QTLs associated with root traits using two different populations in wheat (*Triticum aestivum* L.). *Euphytica* 206:175–190.
- King, J., Gay, A., Sylvester-Bradley, R., Bingham, I., Foulkes, J., Gregory, P., and Robinson, D. (2003). Modelling cereal root systems for water and nitrogen capture: towards an economic optimum. *Ann Bot.* 91:383–390.
- Kitomi, Y., Kanno, N., Kawai, S., Mizubayashi, T., Fukuoka, S., and Uga, Y. (2015). QTLs underlying natural variation of root growth angle among rice varieties with the same functional allele of *DEEPER ROOTING 1*. *Rice* 8:16.
- Komyshchev, E., Genaev, M. and Afonnikov, D. (2017). Evaluation of the SeedCounter, A Mobile Application for Grain Phenotyping. *Front. Plant Sci.* 7:1990.
- Kris-Etherton, P.M., Lefevre, M., Beecher, G.R., Gross, M.D., Keen, C.L. and Etherton, T.D. (2004). Bioactive compounds in nutrition and health-research methodologies for establishing biological function: the antioxidant and anti-inflammatory effects of flavonoids on atherosclerosis. *Annu Rev Nutr* 4:511–38.

- Kruglyak, L. (1999). Prospects for whole-genome linkage disequilibrium mapping of common disease genes. *Nat Genet* 22:139–144.
- Kubo, K., Elouafi, L., Watanabe, N., Nachit, M.M., Inagaki, M.N., Iwama, K., and Jitsuyama, Y. (2007). Quantitative trait loci for soil-penetrating ability of roots in durum wheat. *Plant Breeding* 126:375–378.
- Kubo, K., Jitsuyama, Y., Iwama, K., Hasegawa, T. and Watanabe, N. (2004). Genetic difference in root penetration ability by durum wheat (*Triticum turgidum* L. var. *durum*) evaluated by a pot with paraffin-Vaseline discs. *Plant Soil* 262:169–177.
- Kumar, A., Mantovani, E. E., Seetan, R., Soltani, A., Echeverrysolarte, M., Jain, S., et al. (2016). Dissection of genetic factors underlying wheat kernel shape and size in an elite non-adapted cross using a high density SNP linkage map. *Plant Genome* 9:2–22.
- Kump, K.L., Bradbury, P.J., Wissner, R.J., Buckler, E.S., Belcher, A.R., Oropeza–Rosas, M.A., et al. (2011). Genome-wide association study of quantitative resistance to southern leaf blight in the maize nested association mapping population. *Nat Genet* 43:163–168.
- Laido, G., Mangini, G., Taranto, F., Gadaleta, A., Blanco, A., Cattivelli, L., et al. (2013). Genetic Diversity and Population Structure of Tetraploid Wheats (*Triticum turgidum* L.) Estimated by SSR, DArT and Pedigree Data. *Plos One* 8.
- Landjeva, S., Korzun, V. and Borner, A. (2007). Molecular markers: actual and potential contributions to wheat genome characterization and breeding. *Euphytica* 156:271–296.
- Landi, P., Giuliani, S., Salvi, S., Ferri, M., Tuberosa, R., and Sanguineti, M.C. (2010). Characterization of *root-yield-1.06*, a major constitutive QTL for root and agronomic traits in maize across water regimes. *J. Exp. Bot.* 61:3553–3562.

- Laperche, A., Devienne-Barret, F., Maury, O., Le Gouis, J., and Ney, B. (2006). A simplified conceptual model of carbon/nitrogen functioning for QTL analysis of winter wheat adaptation to nitrogen deficiency. *Theor Appl Genet.* 113:1131–1146.
- Leopold, A.C. (1990). Coping with desiccation. In: Alscher RG and Cumming JR. Stress Responses in plants: Adaptation and Acclimation Mechanisms. Wiley-Liss, New York. pp. 37–56.
- Letta, T., Maccaferri, M., Badebo, A., Ammar, K., Ricci, A., Crossa, J. and Tuberosa, R. (2013). Searching for novel sources of field resistance to Ug99 and Ethiopian stem rust races in durum wheat via association mapping. *Theor. Appl. Genet.* 126(5):1237–56.
- Levy, A.A. and Feldman, M. (1989). Location of genes for high grain protein percentage and other quantitative traits in wild wheat *Triticum turgidum* var. *dicoccoides*. *Euphytica* 41:113–122.
- Li, H., Peng, Z., Yang, X., Wang, W., Fu, J., Wang J., et al. (2013). Genome-wide association study dissects the genetic architecture of oil biosynthesis in maize kernels. *Nat. Genet.* 45(1):43–50
- Li, P., Chen, F., Cai, H., Liu, J., Pan, Q., Liu, Z., Gu, R., Mi, G., Zhang, F., and Yuan, L. (2015). A genetic relationship between nitrogen use efficiency and seedling root traits in maize as revealed by QTL analysis. *J. Exp. Bot.* 66:3175–3188.
- Li, Q., Yang, X.H., Xu, S.T., Cai, Y., Zhang, D.L., Han, Y.J., et al. (2012). Genome-wide association studies identified three independent polymorphisms associated with alpha-tocopherol content in maize kernels. *PLoS ONE* 7(5):e36807.

- Li, W.H., Liu, W., Liu, L., You, M.S., Liu, G.T. and Li, B.Y. (2011). QTL mapping for wheat flour color with additive, epistatic, and QTL $\times$ environmental interaction effects. *Agr Sci China* 10:651–660.
- Li, Y., Cheng, R.Y., Spokas, K.A., Palmer, A.A. and Borevitz, J.O. (2014). Genetic variation for life history sensitivity to seasonal warming in *Arabidopsis thaliana*. *Genetics* 196:569–577.
- Li, Y., Huang, Y., Bergelson, J., Nordborg, M. and Borevitz, J.O. (2010). Association mapping of local climate-sensitive quantitative trait loci in *Arabidopsis thaliana*. *Proc Natl Acad Sci U S A* 107(49):21199–21204.
- Liao, M., Fillery, I. R. P., and Palta, J. A. (2004). Early vigorous growth is a major factor influencing nitrogen uptake in wheat. *Funct Plant Biol.* 31:121–129.
- Liu, K.J. and Muse, S.V. (2005). PowerMarker: an integrated analysis environment for genetic marker analysis. *Bioinformatics* 21:2128–2129.
- Liu, W., Maccaferri, M., Rynearson, S., Letta, T., Zegeye, H., Tuberosa, R., et al. (2017). Novel Sources of Stripe Rust Resistance Identified by Genome-Wide Association Mapping in Ethiopian Durum Wheat (*Triticum turgidum* ssp. durum). *Front. Plant Sci.* 8:774. doi: 10.3389/fpls.2017.00774
- Liu, X., Li, R., Chang, X. and Jing, R. (2013). Mapping QTLs for seedling root traits in a doubled haploid wheat population under different water regimes. *Euphytica* 189:51–66. doi: 10.1007/s10681-012-0690-4
- Lobet, G., Couvreur, V., Meunier, F., Javaux M. and Draye, X. (2014). Plant water uptake in drying soils. *Plant Physiol.* 164:1619–1627.
- Long, N.V., Dolstra, O., Malosetti, M., Kilian, B., Graner, A., Visser, R.G.F. and van der Linden, C.G. (2013). Association mapping of salt tolerance in barley (*Hordeum vulgare* L.). *Theor Appl Genet* 126:2335–2351.

- Lorenz, A.J., Hamblin, M.T. and Jannink, J.L. (2010). Performance of single nucleotide polymorphisms versus haplotypes for genome-wide association analysis in barley. *PLoS ONE* 5(11):e14079.
- Lucas, M.R., Huynh, B.L., Vinholes, P.S., Cisse, N., Drabo, I., Ehlers, J.D., et al. (2013). Association studies and legume synteny reveal haplotypes determining seed size in *Vigna unguiculata*. *Front Plant Sci.* 4:1–9.
- Lynch, J.P. (2013). Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Ann Bot.* 112:347–357.
- Lynch, J.P. and Wojciechowski, T. (2015). Opportunities and challenges in the subsoil: pathways to deeper rooted crops. *J. Exp. Bot.* 66:2199–2210.
- Lynch, M. and Walsh, B. (1998). Genetics and analysis of quantitative traits. Sinauer Press, Sunderland, 980.
- Ma, M., Wang, Q., Li, Z., Cheng, H., Li, Z., Liu, X., et al. (2015). Expression of *TaCYP78A3*, a gene encoding cytochrome P450 CYP78A3 protein in wheat (*Triticum aestivum* L.), affects seed size. *Plant J.* 83:312–325.
- Maccaferri, M., Canè, M.A., Sanguineti, M.C., Salvi, S., Colalongo, M.C., and Massi, M. et al. (2014). A consensus framework map of durum wheat (*Triticum durum* Desf.) suitable for linkage disequilibrium analysis and genome-wide association mapping. *BMC Genomics* 15:873. doi:10.1186/1471-2164-15-873
- Maccaferri, M., EI-Feki, W., Nazemi, G., Salvi, S., Canè, M. A., Colalongo, M. C., et al. (2016). Prioritizing quantitative trait loci for root system architecture in tetraploid wheat. *J. Exp. Bot.* 67:1161–1178. doi: 10.1093/jxb/erw039
- Maccaferri, M., Harris, N. S., Twardziok, S.O., Pasam, R.K., Gundlach, H., Spannag, S. et al., (2019). Durum wheat genome highlights past domestication signatures and future improvement targets. *Nature Genetics* 51:885–895.

- Maccaferri, M., Ricci, A., Salvi, S., Milner, S.G., Noli, E., Martelli, P.L. *et al.* (2015). A high-density, SNP-based consensus map of tetraploid wheat as a bridge to integrate durum and bread wheat genomics and breeding. *Plant Biotechnol J.* 13:648–663.
- Maccaferri, M., Sanguineti, M. C., Donini, P. and Tuberosa, R. (2003). Microsatellite analysis reveals a progressive widening of the genetic basis in the elite durum wheat germplasm. *Theor. Appl. Genet.* 107:783–797.
- Maccaferri, M., Sanguineti, M., Noli, E. and Tuberosa, R. (2005). Population structure and long-range disequilibrium in a durum wheat elite collection. *Mol Breed* 15:271–290.
- Maccaferri, M., Sanguineti, M.C., del Moral, L.F.G., Demontis, A., El–Ahmed, A., Maalouf, F., *et al.* (2011). Association mapping in durum wheat grown across a broad range of water regimes and yield potential. *J. Exp. Bot.* 62:409–438.
- Mace, E.S., Singh, V., Van Oosterom, E.J., Hammer, G.L., Hunt, C.H. and Jordan, D.R. (2012). QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. *Theor Appl Genet.* 124:97–109.
- Mackay, L. and Powell, W. (2007). Methods for linkage disequilibrium mapping in crops. *Trends Plant Sci* 12:57–63.
- Mann, M.L. and Warner, J.M. (2017). Ethiopian wheat yield and yield gap estimation: A spatially explicit small area integrated data approach. *Field Crops Res* 201:60–74.
- Manolio, T.A., Collins, F.S., Cox, N.J., Goldstein, D.B., Hindorff, L.A., Hunter, D.J., *et al.* (2009). Finding the missing heritability of complex diseases. *Nature* 461:747–753.

- Manschadi, A.A., Hammer, G.L., Christopher, J.T., and deVoil, P. (2008). Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). *Plant Soil* 303:115–129.
- Mares, D.J. and Campbell, A.W. (2001). Mapping components of flour and noodle color in Australian wheat. *Australian Journal of Agricultural Research* 52:1297–1309.
- Mascher, M., Richmond, T.A., Gerhardt, D.J., Himmelbach, A., Clissold, L., Sampath, D., et al. (2013). Barley whole exome capture: a tool for genomic research in the genus *Hordeum* and beyond. *Plant J.* 76(3):494–505.
- Mayer, K.F., Rogers, J., Doležal, J., Pozniak, C., Eversole, K., Feuillet, C., et al. (2014). A chromosome-based draft sequence of the hexaploid bread wheat (*Triticum aestivum*) genome. *Science* 345(6194):1251788.
- Mazza, G. (2000). Health aspects of natural colors. In ‘Natural food colorants—science and technology’. (Eds GJ Lauro, FJ Francis) pp. 289–314. (Marcel Dekker: New York)
- McNally, K.L., Childs, K.L., Bohnert, R., Davidson, R.M., Zhao, K., Ulat, V.J., et al. (2009). Genome-wide SNP variation reveals relationships among landraces and modern varieties of rice. *Proc. Natl. Acad. Sci. USA* 106(30):12273–8.
- McWilliam, J. (1989). The dimensions of drought. In: Baker F, ed. Drought resistance in cereals. Wallingford, UK: CAB International, 1–11.
- Meister, R., Rajani, M.S., Ruzicka, D. and Schachtman, D.P. (2014). Challenges of modifying root traits in crops for agriculture. *Trends Plant Sci.* 19:779–788.
- Mengistu, D. K., and Pè, M. E. (2016). Revisiting the ignored Ethiopian durum wheat (*Triticum turgidum* var. durum) landraces for genetic diversity exploitation in future wheat breeding programs. *J. Plant Breed. Crop Sci.* 8:45–59.

- Mengistu, D. K., Kidane, Y. G., Catellani, M., Frascaroli, E., Fadda, C., Pè, M. E., et al. (2016). High-density molecular characterization and association mapping in Ethiopian durum wheat landraces reveals high diversity and potential for wheat breeding. *Plant Biotechnol. J.* 14:1800–1812. doi: 10.1111/pbi.12538
- Mengistu, D. K., Kiros, A.Y., and Pè, M. E. (2015). Phenotypic diversity in Ethiopian durum wheat (*Triticum turgidum* var. durum) landraces. *Crop J.* 3:190–199.
- Mengistu, D.K., Kidane, Y.G., Fadda, C. and Pie, M.E. (2018). Genetic diversity in Ethiopian durum wheat (*Triticum turgidum* var durum) inferred from phenotypic variations. *Plant Genet. Resour. Charact. Util.* 16:39–49.
- Meuwissen, T.H.E, Hayes, B. and Goddard, M.E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157:1819–1829.
- Mickelbart, M.V., Hasegawa, P.M., and Bailey-Serres, J. (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nat Rev Genet.* 16:237–251. doi: 10.1038/nrg3901
- Miguel, M.A., Postma, J.A. and Lynch, J.P. (2015). Phen synergism between root hair length and basal root growth angle for phosphorus acquisition. *Plant Physiol* 167:1430–1439. doi: 10.1104/pp.15.00145
- Millet, E., Rong, J.K., Qualset, C.O., McGuire, P.E., Bernard, M., Sourdille, P. and Feldman, M. (2013). Production of chromosome-arm substitution lines of wild emmer in common wheat. *Euphytica* 190:1–17.
- Moeller, S.M., Jacques, P.F. and Blumberg, J.B. (2000). The potential of dietary xanthophylls in cataract and age-related macular degeneration. *Journal of the American College of Nutrition* 19:522S–527S.
- Moragues, M., Moralejo, M., Sorrells, M.E., Royo, C. (2007). Dispersal of durum wheat [*Triticum turgidum* L. ssp. *turgidum* convar. *durum* (Desf.) MacKey]

- landraces across the Mediterranean basin assessed by AFLPs and microsatellites. *Genet. Resour. Crop Evol.* 54:1133–1144.
- Morris, G.P., Ramu, P., Deshpande, S.P., Hash, C.T., Shah, T., Upadhyaya, H.D., et al. (2012). Population genomic and genome-wide association studies of agro-climatic traits in sorghum. *Proc. Natl. Acad. Sci. USA* 110(2):453–58
- Muchero, W., Roberts, P.A., Diop, N.N., Drabo, I., Cisse, N., Close, T. et al. (2013). Genetic architecture of delayed senescence, biomass, and grain yield under drought stress in cowpea. *PLoS ONE* 8(7):e70041.
- Munoz–Amatriain, M., Cuesta–Marcos, A., Endelman, J.B., Comadran, J., Bonman, J.M., Bockelman, H.E., et al. (2014). The USDA barley core collection: genetic diversity, Population structure, and potential for genome–wide association studies. *PLoS ONE* 9(4):e94688.
- Nakhforoosh, A., Grausgruber, H., Kaul, H.P. and Bodner, G. (2015). Dissection of drought response of modern and underutilized wheat varieties according to Passioura's yield- water framework. *Front. Plant Sci* 6:570.
- Nalam, V.J., Vales, M.I., Watson, C.J., Kianian, S.F. and Riera-Lizarazu, O. (2006). Map-based analysis of genes affecting the brittle rachis character in tetraploid wheat (*Triticum turgidum* L.). *Theor. Appl. Genet.*, 112:373–381.
- Narayanan, S., Mohan, A., Gill, K. S., and Prasad, P. V. (2014). Variability of root traits in spring wheat germplasm. *PLoS One* 9:e100317.
- Naz, A., Arifuzzaman, M., Muzammil, S., Pillen, K. and León, J. (2014). Wild barley introgression lines revealed novel QTL alleles for root and related shoot traits in the cultivated barley (*Hordeum vulgare* L.). *BMC Genet.* 15:107.
- Negassa, A., Koo, J., Sonder, K., Shiferaw, B., Smale, M., Braun, H., et al. (2012). The Potential for Wheat Production in Sub-Saharan Africa: Analysis of

- Biophysical Suitability and Economic Profitability, Pre-print galley for circulation at the conference “Wheat for food security in Africa: Science and policy dialogue about the future of wheat in Africa”, Addis Ababa, Ethiopia, Oct. 08–12.
- Nei, M. (1972). Genetic Distance between Populations. *The American Naturalist* 106: 283–292.
- Nei, M. (1978). Estimation of Average Heterozygosity and Genetic Distance from a Small Number of Individuals. *Genetics* 89:583–590.
- Nemri, A., Atwell, S., Tarone, A.M., Huang, Y.S., Zhao, K., Studholme, D.J., et al. (2010). Genome-wide survey of Arabidopsis natural variation in downy mildew resistance using combined association and linkage mapping. *Proc Natl Acad Sci U S A* 107(22):10302–10307.
- Newell, M.A., Asoro, F.G., Scott, M.P., White, P.J., Beavis, W.D. and Jannink, J.L. (2012). Genome-wide association study for oat (*Avena sativa* L.) betaglucan concentration using germplasm of worldwide origin. *Theor Appl Genet* 125:1687–1696.
- Ng, S.B., Turner, E.H., Robertson, P.D., Flygare, S.D., Bigham, A.W., Lee, C., et al. (2009). Targeted capture and massively parallel sequencing of 12 human exomes. *Nature* 461(7261):272–76
- Nishino, H., Murakoshi, M., Tokuda, H. and Yoshiko, S. (2009). Cancer prevention by carotenoids. *Archives of Biochemistry and Biophysics* 483:165–168.
- Nordborg, M, Hu TT, Ishino Y, Jhaveri J, Toomajian, C., Zheng, H., et al. (2005). The pattern of polymorphism in Arabidopsis thaliana. *PLoS Biol* 3(7):e196.
- Nordborg, M., Borevitz, J.O., Bergelson, J., Berry, C.C., Chory, J. Hagenblad, J., et al., (2002). The extent of linkage disequilibrium in *Arabidopsis thaliana*. *Nat Genet* 30(2):190–193

- Oliver, J.R., Blakeney, A.B. and Allen, H.M. (1992). Measurement of flour color in color space parameters. *Cereal Chem* 69:546–551
- Ortiz, R., Iwanaga, M., Reynolds, M.P., Wu, H. and Crouch, J.H. (2007). Overview on crop genetic engineering for drought-prone environments. *J. Semi-Arid Trop. Agric. Res.* 4:1.
- Osborne, B. G. and Anderssen, R. S. (2003). Single-kernel characterization principles and applications. *Cereal Chem. J.* 80:613–622.
- Osmont, K.S., Sibout, R. and Hardtke, C.S. (2007). Hidden branches: developments in root system architecture. *Annu. Rev. Plant. Biol.* 58:93–113.
- Palaisa, K.A., Morgante, M., Williams, M. and Rafalski, A. (2003). Contrasting effects of selection on sequence diversity and linkage disequilibrium at two phytoene synthase loci. *Plant Cell* 15:1795–1806
- Palozza, P. and Krinsky, N.I. (1992). Antioxidant effects of carotenoids in vivo and in vitro: an overview. *Methods in Enzymology* 213:403–452.
- Pasam, R.K., Sharma, R., Malosetti, M., van Eeuwijk, F.A., Haseneyer, G., Kilian, B. and Graner, B. (2012). Genome-wide association studies for agronomical traits in a worldwide spring barley collection. *BMC Plant Biol.* 12:16
- Passioura, J.B. (2010). Scaling up: the essence of effective agricultural research. *Funct. Plant Biol.* 37:585–591.
- Patel, K.K., Jain, A. and Patel, D.K. (2013). Medicinal significance, pharmacological activities, and analytical aspects of anthocyanidins ‘delphinidin’: A concise report. *J Acute Dis.* 2:169–178.
- Pecetti, L., Annicchiarico, P. and Damania, A.B. (1992). Biodiversity in a germplasm collection of durum wheat. *Euphytica* 60:229–238.

- Peleg, Z., Fahima, T., Abbo, S., Krugman, T. and Saranga, Y. (2008). Genetic structure of wild emmer wheat populations as reflected by transcribed versus anonymous SSR markers. *Genome* 51:187–195.
- Peleg, Z., Fahima, T., Korol, A.B., Abbo, S. and Saranga, Y. (2011). Genetic analysis of wheat domestication and evolution under domestication. *J. Exp. Bot.* 62:5051–5061.
- Peleg, Z., Fahima, T., Krugman, T., Abbo, S., Yakir, D., Korol, A.B. and Saranga, Y. (2009). Genomic dissection of drought resistance in durum wheat x wild emmer wheat recombinant inbred line population. *Plant. Cell Environ.* 32:758–779.
- Peng, J., Ronin, Y., Fahima, T., Roder, M.S., Li, Y., Nevo, E. and Korol, A. (2003). Domestication quantitative trait loci in *Triticum dicoccoides*, the progenitor of wheat. *Proc. Natl. Acad. Sci. USA* 100:2489–2494.
- Peng, J.H., Sun, D. and Nevo, E. (2011). Domestication evolution, genetics and genomics in wheat. *Mol. Breed.* 28:281–301.
- Perrier, X. and Jacquemoud-Collet, J. P. (2006). DARwin software. <http://darwin.cirad.fr/> Accessed 20 March 2019.
- Peterson, C.J., Graybosch, R.A., Shelton, D.R. and Baenziger, P.S. (1998). Baking quality of hard winter wheat: Response of genotypes to environment in the Great Plains. *Euphytica* 100:157–162.
- Peterson, G.W., Dong, Y., Horbach, C. and Fu, Y.B. (2014). Genotyping-by-sequencing for plant genetic diversity analysis: a lab guide for SNP genotyping. *Diversity* 6:665–680.
- Petrarulo, M., Marone, D., Ferragonio, P., Cattivelli, L., Rubiales, D., De Vita, P., and Mastrangelo, A.M. (2015). Genetic analysis of root morphological traits in wheat. *Mol Genet Genomics* 290:785–806. doi: 10.1007/s00438-014-0957-7

- Pinto, R.S. and Reynolds, M.P. (2015). Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. *Theor. Appl. Genet.* 128:575–585.
- Porceddu, E., Perrino, P. and Olita, G. (1973). Preliminary information on an Ethiopian wheat germplasm collecting mission. pp. 181-200 in Proceedings of the Symposium on genetics and breeding of durum wheat, 14-18 May 1973, Bari, Italy (G.T. Scarascia Mugnozza, ed.). University of Bari, Italy.
- Pozniak, C.J., Knox, R.E., Clarke, F.R. and Clarke, J.M. (2007). Identification of QTL and association of a phytoene synthase gene with endosperm color in durum wheat. *Theor. Appl. Genet.* 114:525–537.
- Price, A.L., Patterson, N.J., Plenge, R.M., Weinblatt, M.E., Shadick, N.A. and Reich, D. (2006). Principal components analysis corrects for stratification in genome-wide association studies. *Nat. Genet.* 38:904–909.
- Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Pryce, J.E., Bolormaa, S., Chamberlain, A.J., Bowman, P.J., Savin, K., Goddard, M.E. and Hayes, B.J. (2010). A validated genome-wide association study in 2 dairy cattle breeds for milk production and fertility traits using variable length haplotypes. *J. Dairy. Sci.* 93(7):3331–3345.
- Putterill, J., Robson, F., Lee, K., Simon, R. and Coupland, G. (1995). The constant gene of *Arabidopsis* promotes flowering and encodes a protein showing similarities to zinc-finger transcription factors. *Cell* 80:847–857.
- R Development Core Team (2013). R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna Austria 0: {ISBN} 3-900051-07-0.

- Ramya, P., Chaubal, A., Kulkarni, K., Gupta, L., Kadoo, N., Dhaliwal, H. S., et al. (2010). QTL mapping of 1000-kernel weight, kernel length, and kernel width in bread wheat (*Triticum aestivum* L.). *J. Appl. Genet.* 51:421–429.
- Rasheed, A., Xia, X., Ogbonnaya, F., Mahmood, T., Zhang, Z., Mujeeb-Kazi, A. and He, Z. (2014). Genome-wide association for grain morphology in synthetic hexaploid wheats using digital imaging analysis. *BMC Plant Biology* 14:128.
- Ren, J., Sun, D., Chen, L., You, F.M., Wang, J., Peng, Y., Nevo, E. et al. (2013). Genetic diversity revealed by single nucleotide polymorphism markers in a worldwide germplasm collection of durum wheat. *Int. J. Mol. Sci.* 14:7061–7088.
- Ren, Y. Z., He, X., Liu, D. C., Li, J. J., Zhao, X. Q., Li, B., et al. (2012). Major quantitative trait loci for seminal root morphology of wheat seedlings. *Mol. Breeding* 30:139–148. doi: 10.1007/s11032-011-9605-7
- Ren, Y., Qian, Y., Xu, Y., Zou, C., Liu, D., Zhao, X., Zhang, A. and Tong, Y. (2017) Characterization of QTLs for Root Traits of Wheat Grown under Different Nitrogen and Phosphorus Supply Levels. *Front. Plant Sci.* 8:2096.
- Reynolds, M. and Tuberosa, R. (2008). Translational research impacting on crop productivity in drought-prone environments. *Curr. Opin. Plant Biol.* 11:171–179.
- Ribaya-Mercado, J.D. and Blumberg, J.B. (2004). Lutein and zeaxanthin and their potential roles in disease prevention. *Journal of the American College of Nutrition* 23:567S–587S.
- Richard, C.A., Hickey, L.T., Fletcher, S., Jennings, R., Chenu, K., and Christopher, J.T. (2015). High-throughput phenotyping of seminal root traits in wheat. *Plant Methods* 11:13. doi: 10.1186/s13007-015-0055-9
- Risch, N. and Merikangas, K. (1996). The future of genetic studies of complex human diseases. *Science* 273:1516–1517.

- Röder, M. S., Huang, X. Q. and Börner, A (2008). Fine mapping of the region on wheat chromosome 7D controlling grain weight. *Funct Integr Genomics*. 8:79–86.
- Rogers, J.S. (1972). Measures of genetic similarity and genetic distance: Studies in genetics. VII. Univ. Texas Publ. 7213:145–153.
- Romay, M.C., Millard, M.J., Glaubitz, J.C., Peiffer, J.A., Swarts, K.L., Casstevens, T.M., et al. (2013). Comprehensive genotyping of the USA national maize inbred seed bank. *Genome Biol* 14:R55.
- Roncallo, P. F., Cervigni, G. L., Jensen, C., Miranda, R., Carrera, A. D., Helguera, M., et al. (2012). QTL analysis of main and epistatic effects for flour color traits in durum wheat. *Euphytica* 185:77–92.
- Rosas, U., Cibrian–Jaramillo, A., Ristova, D., Banta, J.A., Gifford, M.L., Fan, A.H., et al. (2013). Integration of responses within and across Arabidopsis natural accessions uncovers loci controlling root systems architecture. *Proc Natl Acad Sci* 110(37):15133–15138.
- Ruan, X., Wang, W., Kong, J., Yu, F. and Huang, X., (2010). Genetic linkage mapping of turbot (*Scophthalmus maximus* L.) using microsatellite markers and its application in QTL analysis. *Aquaculture* 308:89–100.
- Russo, M.A., Ficco, D.B.M., Laido, G., Marone, D., Papa, R., . Blanco, A. et al. (2014). A dense durum wheat $\times$ *T. dicoccum* linkage map based on SNP markers for the study of seed morphology. *Mol. Breed.* 34:1579–1597.
- Saidou, A.A., Clotault, J., Couderc, M., Mariac, C., Devos, K.M., Thuillet, A.C., et al. (2014). Association mapping, patterns of linkage disequilibrium and selection in the vicinity of the PHYTOCHROME C gene in pearl millet. *Theor Appl Genet* 127:19–32.

- Sakamoto, S. and Fukui, K. (1972) Collection and preliminary observation of cultivated cereals and legumes in Ethiopia. *Kyoto Univ. Afr. Stud.* 7:181–225.
- Salamini, F., Ozkan, H., Brandolini, A., Schafer-Pregl, R. and Martin, W. (2002). Genetics and geography of wild cereal domestication in the near east. *Nat. Rev. Genet.* 3:429–441.
- Sanguineti, M. C., Li, S., Maccaferri, M., Corneti, S., Rotondo, F., Chiari, T., et al. (2007). Genetic dissection of seminal root architecture in elite durum wheat germplasm. *Ann. Appl. Biol.* 151, 291–305. doi: 10.1111/j.1744-7348.2007.00198
- Sauvage, C., Segura, V., Bauchet, G., Stevens, R., Do, P.T., Nikoloski, Z. et al. (2014). Genome-wide association in tomato reveals 44 candidate loci for fruit metabolic traits. *Plant Physiol* 165:1120–1132.
- Schneeberger, K. and Weigel, D. (2011). Fast-forward genetics enabled by new sequencing technologies. *Trends Plant Sci.* 16:282–88.
- Seboka, B. and Deressa, A. (1999). Validating farmers' indigenous social networks for local seed supply in central rift valley of Ethiopia. *J. Agric. Educ. Ext.* 6:245–254.
- Sharma, S., Chunduri, V., Kumar, A., Kumar, R., Khare, P., Kondepudi, K.K, et al. (2018). Anthocyanin bio-fortified colored wheat: Nutritional and functional characterization. *PLoS ONE* 13:e0194367
- Sherman, J. D., Souza, E., See, D. and Talbert, L. E. (2008). Microsatellite Markers for Kernel Color Genes in Wheat. *Crop Science* 48:1419–424
- Shirasawa, K., Fukuoka, H., Matsunaga, H., Kobayashi, Y., Kobayashi, I., Hirakawa, H. et al. (2013). Genome-wide association studies using single nucleotide polymorphism markers developed by re-sequencing of the genomes of cultivated tomato. *DNA Res* 20:593–603.

- Shu, X. and Rasmussen, S.K. (2014). Quantification of amylose, amylopectin and b-glucan in the search for genes controlling the three major quality traits in barley using genome-wide association studies. *Front Plant Sci* 5:197.
- Simons, K.J., Fellers, J.P., Trick, H.N., Zhang, Z., Tai, Y.S., Gill, B.S. and Faris, J.D. (2006). Molecular characterization of the major wheat domestication gene Q. *Genetics* 172:547–555.
- Siol, M., Jacquin, F., Chabert-Martinello, M., Smýkal, M., Le Paslier, M., Aubert, G. and Burstin, J. (2017). Patterns of Genetic Structure and Linkage Disequilibrium in a Large Collection of Pea Germplasm. *G3–Genes Genom Genet* 7(8):2461–2471.
- Slafer, G.A., Satorre, E.H. and Andrade, F.H. (1994). Increases in grain yield in bread wheat from breeding and associated physiological changes. In: Slafer GA (Ed.), Genetic improvement of field crops. New York: Marcel Dekker Inc., 1–68.
- Slovak, R., Goschl, C., Su, X., Shimotani, K., Shiina, T. and Busch, W. (2014). A scalable open-source pipeline for large-scale root phenotyping of Arabidopsis. *Plant Cell* 26(6):2390–2403.
- Smith, S. and De Smet, I. (2012). Root system architecture: insights from Arabidopsis and cereal crops. *Phil. Trans. R. Soc. B.* 367:1441–1452.
- Sneller, C.H., Mather, D.E. and Crepieux, S. (2009). Analytical Approaches and Population Types for Finding and Utilizing QTL in Complex Plant Populations. *Crop Science* 49:363–380.
- Spalding, E. P. and Miller, N. D. (2013). Image analysis is driving a renaissance in growth measurement. *Curr. Opin. Plant Biol.* 16:100–104.
- Steele, K.A., Price, A.H., Witcombe, J.R., Shrestha, R., Singh, B.N., Gibbons, J.M., and Virk, D.S. (2013). QTLs associated with root traits increase yield in upland

- rice when transferred through marker-assisted selection. *Theor Appl Genet.* 126:101–108.
- Su, Q., Zhang, X., Zhang W, Zhang, N., Song, L., Liu, L., et al. (2018). QTL Detection for Kernel Size and Weight in Bread Wheat (*Triticum aestivum* L.) Using a High-Density SNP and SSR-Based Linkage Map. *Front. Plant Sci.* 91–484.
- Su, Z., Hao, C., Wang, L., Dong, Y. and Zhang, X. (2011). Identification and development of a functional marker of TaGW2 associated with grain weight in bread wheat (*Triticum aestivum* L.). *Theor Appl Genet* 122:211–223.
- Sukumaran, S., Dreisigacker, S., Lopes, M., Chavez, P. and Reynolds, M.P. (2015). Genome-wide association study for grain yield and related traits in an elite spring wheat population grown in temperate irrigated environments. *Theor Appl Genet.* 128:353–63.
- Tabor, H. K., Risch, N. J. and Myers, R. M. (2002). Candidate–gene approaches for studying complex genetic traits: practical considerations. *Nat. Rev. Genet.* 3(5):1–7.
- Tanabata, T., Shibaya, T., Hori, K., Ebana, K. and Yano, M. (2012). SmartGrain: highthroughput phenotyping software for measuring seed shape through image analysis. *Plant Physiol* 160:1871–1880.
- Teklu, Y. and Hammer, K. (2008). Diversity of Ethiopian durum wheat germplasm: breeding opportunities for improving grain yield potential and quality traits. *Plant Genet. Resour* 7:1–8. doi: 10.1017/S1479262108994223
- Teklu, Y., Hammer, K., Huang, X.Q. and Röder, M.S. (2006). Analysis of microsatellite diversity in Ethiopian tetraploid wheat landraces. *Genet. Resour. Crop Evol.* 53:1115–1126. doi: 10.1007/s10722-005-1146-7

- Tesemma, T. and Bechere, E. (1998). Developing elite durum wheat landrace selections (composites) for Ethiopian peasant farm use: raising productivity while keeping diversity alive. *Euphytica* 102:323–328. doi: 10.1023/A:1018360432426
- Tesemma, T. and Belay, G. (1991). Aspects of Ethiopian tetraploid wheats with emphasis on durum wheat genetics and breeding research. In: Wheat Research in Ethiopia: A Historical Perspective (Gebre-Mariam, H., Tanner, D.G. and Hulluka, M., eds), pp. 47–71. Addis Ababa: IAR/CIMMYT.
- Tesfaye, T., Becker, H.C., Belay, G., Mitiku, D., Bechere, E. and Tsegaye, S. (1993). Performance of Ethiopian tetraploid wheat landraces at their collection sites. *Euphytica* 71:221–230.
- Trachsel, S., Kaeppler, S.M., Brown, K.M. and Lynch, J.P. (2011). Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant Soil* 341:75–78.
- Troccoli, A., Borrelli, G.M., DeVita, P., Fares, C. and Di Fonzo, N. (2000). Durum wheat quality: a multidisciplinary concept. *J. Cereal Sci.* 32: 99–113.
- Tsilo, T. J., Hareland, G. A., Chao, S. and Anderson, J. A. (2011). Genetic mapping and QTL analysis of flour color and milling yield related traits using recombinant inbred lines in hard red spring wheat. *Crop Sci.* 51:237–246.
- Tsuda, T., Horio, F., Uchida, K., Aoki, H. and Osawa, T. (2003). Dietary cyanidin 3-O-beta-D-glucoside-rich purple corn color prevents obesity and ameliorates hyperglycemia in mice. *J Nutr.* 133(7):2125–30.
- Tuberosa, R. (2012). Phenotyping for drought tolerance of crops in the genomics era. *Front Physiol* 3:347. doi: 10.3389/fphys.2012.00347
- Tuberosa, R. and Maccaferri, M. (2015). Genomics Approaches to Dissect the Genetic Basis of Drought Resistance in Durum Wheat. In: Advances in Wheat

- Genetics: From Genome to Field. Proceedings of the 12th International Wheat Genetics Symposium. PP: 213–223.
- Tuberosa, R. and Pozniak, C. (2014). Durum wheat genomics comes of age. Introduction to the special issue on durum wheat genomics. *Mol. Breed.* 34:1527–1530.
- Tuberosa, R., Salvi, S., Sanguineti, M.C., Landi, P., Maccaferri, M. and Conti, S. (2002b). Mapping QTLs regulating morpho-physiological traits and yield: case studies, shortcomings and perspectives in drought-stressed maize. *Ann. Bot.* 89:941–963
- Tuberosa, R., Sanguineti, M.C., Landi, P., Giuliani, M.M., Salvi, S. and Conti, S. (2002a). Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Plant. Mol. Biol.* 48:697–712.
- Tuberosa, R., Turner, N. and Cakir, M. (2014). Two decades of Inter Drought conferences: are we bridging the genotype-to-phenotype gap? *J. Exp. Bot.* 65:6137–6139.
- Uga, Y., Kitomi, Y., Ishikawa, S., and Yano, M. (2015). Genetic improvement for root growth angle to enhance crop production. *Breeding sci.* 65:111–119.
- Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., et al. (2013). Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. *Nat. Genet.* 45:1097–1102. doi: 10.1038/srep05563
- Van Inghelandt, D., Melchinger, A.E., Martinant, J.P. and Stich, B. (2012). Genome-wide association mapping of flowering time and northern corn leaf blight (*Setosphaeria turcica*) resistance in a vast commercial maize germplasm set. *BMC Plant Biol* 12:56.

- Vavilov, N.I. (1951). The origin, variation, immunity, and breeding of cultivated plants. Cambridge: Cambridge University Press 1–387.
- von Buren, M. (2001). Polymorphism in two homeologous gamma-gliadin genes and the evolution of cultivated wheat. *Gen. Res. Crop. Evol.* 48:205–220.
- Waines, J. G. and Ehdaie, B. (2007). Domestication and crop physiology: roots of Green-Revolution wheat. *Ann Bot.* 100:991–998. doi: 10.1093/aob/mcm180
- Wang, H., Chattopadhyay, A., Li, Z., Daines, B., Li, Y., Gao, C., et al. (2010). Rapid identification of heterozygous mutations in *Drosophila melanogaster* using genomic capture sequencing. *Genome Res.* 20(7):981–88.
- Wang, S., Zhang, X., Chen, F. and Cui, D. (2015). A Single-Nucleotide Polymorphism of TaGS5 Gene Revealed its Association with Kernel Weight in Chinese Bread Wheat. *Front. Plant Sci.* 6:1166. doi: 10.3389/fpls.2015.01166
- Wang, S.C., Wong, D., Forrest, K., Allen, A., Chao, S., Huang, B.E., et al. (2014). Characterization of polyploid wheat genomic diversity using a high-density 90000 single nucleotide polymorphism array. *Plant Biotechnol J.* 12:787–796.
- Wang, W.Y., Barratt, B.J., Clayton, D.G. and Todd, J.A. (2005). Genome-wide association studies: theoretical and practical concerns. *Nat Rev Genet* 6:109–118.
- Wasson, A.P., Rebetzke, G.J., Kirkegaard, J.A., Christopher, J., Richards, R.A. and Watt, M. (2014). Soil coring at multiple field environments can directly quantify variation in deep root traits to select wheat genotypes for breeding. *J. Exp. Bot.* 65:6231–6249.
- Wasson, A.P., Richards, R.A., Chatrath, R., MiRGA, S.C., Prasad, S.V.S., Rebetzke, G.J., et al. (2012). Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *J. Exp. Bot.* 63:3485–3498.

- Watanabe, N., Sugiyama, K. Yamagishi, Y. and Sakata, Y. (2002). Comparative telosomic mapping of homoeologous genes for brittle rachis in tetraploid and hexaploid wheats. *Hereditas* 137:180–185.
- Westphal, E. (1975). Agricultural systems in Ethiopia. Wageningen: Centre for Agricultural Publishing and Documentation 1–299.
- Williams, K., Munkvold, J. and Sorrells, M (2013). Comparison of digital image analysis using elliptic Fourier descriptors and major dimensions to phenotype seed shape in hexaploid wheat (*Triticum aestivum* L.). *Euphytica* 190:99–116.
- Wojciechowski, T., Gooding, M. J., Ramsay, L., and Gregory, P. J. (2009). The effects of dwarfing genes on seedling root growth of wheat. *J. Exp. Bot.* 60:2565–2573.
- Wu, Q.H., Chen, Y.X., Zhou, S.H., Fu, L., Chen, J.J., Xiao, Y., et al. (2015). High-Density Genetic Linkage Map Construction and QTL Mapping of Grain Shape and Size in the Wheat Population Yanda1817 × Beinong6. *PLoS ONE* 10(2):e0118144.
- Xie, Q., Fernando, K.M., Mayes, S. and Sparkes, D.L. (2017). Identifying seedling root architectural traits associated with yield and yield components in wheat. *Ann Bot.* 119:1115–1129. doi: 10.1093/aob/mcx001
- Xue, Y.D., Warburton, M.L., Sawkins, M., Zhang, X.H., Setter, T., Xu, Y.B., et al. (2013). Genome-wide association analysis for nine agronomic traits in maize under well-watered and water-stressed conditions. *Theor Appl Genet* 126:2587–2596.
- Yan, J., Kandianis, C.B., Harjes, C.E., Bai, L., Kim, E.H., Yang, X., et al. (2010). Rare genetic variation at *Zea mays* crtRB1 increases betacarotene in maize grain. *Nat Genet* 42:322–327.

- Yan, X., Zhao, L., Ren, Y., Dong, Z., Cui, D. and Chen, F. (2019). Genome-wide association study revealed that the TaGW8 gene was associated with kernel size in Chinese bread wheat. *Sci Rep.* 9:2702.
- Yang, W., Duan, L., Chen, G., Xiong, L. and Liu, Q. (2013). Plant phenomics and high-throughput phenotyping: accelerating rice functional genomics using multidisciplinary technologies. *Curr. Opin. Plant Biol.* 16:180–187.
- Yang, W., Guo, Z., Huang, C., Duan, L., Chen, G., Jiang, N., et al. (2014). Combining high-throughput phenotyping and genome-wide association studies to reveal natural genetic variation in rice. *Nat. Commun.* 5:5087.
- Yu, J., Hamblin, M.T. and Tuinstra, M.R. (2013). Association Genetics Strategies and Resources. In: A.H. Paterson (ed.) *Genomics of the Saccharinae*, Plant Genetics and Genomics: Crops and Models. Springer Science + Business Media New York V.11.
- Yu, J., and Buckler, E.S. (2006). Genetic association mapping and genome organization of maize. *Curr. Opin. Biotechnol.* 17:155–160.
- Yu, J., Pressoir, G., Briggs, W.H., Bi, I.V., Yamasaki, M., Doebley, J.F., et al. (2006). A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. *Nat. Genet.* 38: 203–208.
- Zanke, C., Ling, J., Plieske, J., Kollers, S., Ebmeyer, E., Korzun, V., et al. (2014). Genetic architecture of main effect QTL for heading date in European winter wheat. *Front Plant Sci* 5:217.
- Zeven, A.C. (1991). Wheats with purple and blue grains: a review. *Euphytica* 56: 243–258.

- Zhai, S., He, S., Wen, W., Jin, H., Liu, J., Zhang, Y., et al. (2016). Genome-wide linkage mapping of flour color-related traits and polyphenol oxidase activity in common wheat. *Theor Appl Genet* 129(2):377–94
- Zhai, S., Liu, J., Xu, D., Wen, W., Yan, J., Zhang, P., et al. (2018). A Genome-Wide Association Study Reveals a Rich Genetic Architecture of Flour Color-Related Traits in Bread Wheat. *Front. Plant Sci.* 9:1136.
- Zhang, Y. L., Wu, Y. P., Xiao, Y. G., He, Z. H., Zhang, Y., Yan, J., et al. (2009). QTL mapping for flour and noodle color components and yellow pigment content in common wheat. *Euphytica* 165:435–444.
- Zhang, Z., Belcram, H., Gornicki, P., Charles, M., Just, J., Huneau, C., et al. (2011). Duplication and partitioning in evolution and function of homoeologous Q loci governing domestication characters in polyploid wheat. *Proc. Natl. Acad. Sci. USA* 108:18737–18742.
- Zhao, K., Tung, C.W., Eizenga, G.C., Wright, M.H., Ali, M.L., Price, A.H., et al. (2011). Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. *Nat. Commun* 2:467.
- Zhao, Q., Huang, X., Lin, Z. and Han, B. (2010). SEG–Map: a novel software for genotype calling and genetic map construction from next–generation sequencing. *Rice* 3:98–102.
- Zhao, Y., Sun, H.Y., Wang, Y.Y., Pu, Y.Y., Kong, F.M. and Li, S.S. (2013). QTL mapping for the color, carotenoids and polyphenol oxidase activity of flour in recombinant inbred lines of wheat. *Aust J Crop Sci* 7:328–337.
- Zheng, X., Levine, D., Shen, J., Gogarten, S.M., Laurie, C. and Weir, B.S. (2012). A High-performance Computing Toolset for Relatedness and Principal Component Analysis of SNP Data. *Bioinformatics* 15:3326–3328.

- Zhu, J., Kaeppler, S. M. and Lynch, J. P. (2005). Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theor Appl Genet.* 111:688–695.
- Zila, C.T., Samayoa, L.F., Santiago, R., Butron, A. and Holland, J.B. (2013). A genome-wide association study reveals genes associated with Fusarium ear rot resistance in a maize core diversity panel. *G3–Genes Genom Genet* 3:2095–2104.
- Zohary, D. (1970). Centers of diversity and centers of origin. In: Genetic resources of plants- their exploration and conservation. Frankel, O.H. & Bennett, E. (eds.) Blackwell, Oxford. 33–42.
- Zohary, D. and Feldman, M. (1962). Hybridization between amphiploids and the evolution of polyploids in the wheat (*Aegilops-Triticum*) group. *Evolution* 16:44–61.

APPENDICES

Appendix Table 1. Accession names and types, cultivated areas, seed sources and STRUCTURE-inferred clusters of 192 Ethiopian durum wheat accessions.

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP001	WC-1no.4	Landrace	Wollo	DZARC		1	0.833	0.017	0.151
EP002	WC-1no.59	Landrace	Wollo	DZARC		1	0.839	0.016	0.145
EP003	WC-2no.85	Landrace	Wollo	DZARC		3	0.288	0.051	0.661
EP004	WC-4no.2	Landrace	Wollo	DZARC		1	0.992	0.006	0.002
EP005	WC-10no.75	Landrace	Wollo	DZARC		3	0.028	0.041	0.931
EP006	DW-K-Ino.24	Landrace	DZARC(Debre Zeit)	DZARC		3	0.156	0.016	0.829
EP007	DW-K-Ino.96	Landrace	DZARC(Debre Zeit)	DZARC		1	0.931	0.001	0.068
EP008	DW-K-Ino.131	Landrace	DZARC(Debre Zeit)	DZARC		1	0.979	0	0.021
EP009	DW-K-Ino.136	Landrace	DZARC(Debre Zeit)	DZARC		3	0.122	0.001	0.877
EP010	DW-A-Ino.71	Landrace	Akaki(Shewa)	DZARC		3	0.196	0.001	0.804
EP011	DW-A-Ino.80	Landrace	Akaki(Shewa)	DZARC		3	0.165	0.001	0.834
EP012	DW-A-Ino.130	Landrace	Akaki(Shewa)	DZARC		3	0.006	0.012	0.982
EP013	DW-A-4no.17	Landrace	Akaki(Shewa)	DZARC		3	0.001	0	0.999
EP014	DW-A-4no.36	Landrace	Akaki(Shewa)	DZARC		3	0.125	0.001	0.874
EP015	DW-B-3no.28	Landrace	Gojjam(Bichena)	DZARC		3	0.003	0.005	0.992
EP016	DW-B-3no.40	Landrace	Gojjam(Bichena)	DZARC		3	0.042	0.001	0.957
EP017	DW-A-3no.73	Landrace	Akaki(Shewa)	DZARC		3	0.001	0	0.999
EP018	CD-no.32	Landrace	USA	DZARC		3	0.132	0	0.867

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP019	CD-1no.65	Landrace	USA	DZARC		3	0.098	0.007	0.896
EP020	CD-1no.89	Landrace	USA	DZARC		3	0.278	0.001	0.721
EP021	DW-B1no.34	Landrace	Gojjam(Bichena)	DZARC		3	0.143	0.04	0.816
EP022	DW-B1no.98	Landrace	Gojjam(Bichena)	DZARC		1	0.51	0.03	0.46
EP023	Gojam-23no.39	Landrace	Gojjam	DZARC		1	0.675	0.055	0.269
EP024	Gojam-24no.23	Landrace	Gojjam	DZARC		1	0.909	0.001	0.09
EP025	Gojam-24no.33	Landrace	Gojjam	DZARC		1	0.9	0	0.099
EP026	Tigray-8no.7	Landrace	Tigray	DZARC		1	0.985	0.001	0.015
EP028	Tigray-8no.1	Landrace	Tigray	DZARC		1	0.98	0.002	0.018
EP029	Shoa-28no.15	Landrace	Shewa	DZARC		1	0.976	0.001	0.023
EP030	Shoa-28no.17	Landrace	Shewa	DZARC		1	0.862	0	0.137
EP031	Shoa-28no.22	Landrace	Shewa	DZARC		1	0.99	0.002	0.008
EP032	WC-1no.109	Landrace	Wollo	DZARC		3	0.059	0	0.94
EP033	WC-2no.1	Landrace	Wollo	DZARC		3	0.167	0.001	0.832
EP034	WC-2no.12	Landrace	Wollo	DZARC		1	0.616	0.068	0.316
EP036	WC-2no.41	Landrace	Wollo	DZARC		3	0.247	0.001	0.753
EP037	WC-2no.47	Landrace	Wollo	DZARC		1	0.597	0.074	0.329
EP038	WC-2no.58	Landrace	Wollo	DZARC		3	0.295	0.04	0.665
EP039	WC-2no.80	Landrace	Wollo	DZARC		3	0.286	0.04	0.674
EP041	WC-2no.100	Landrace	Wollo	DZARC		1	0.603	0.066	0.33
EP042	WC-4no.78	Landrace	Wollo	DZARC		1	0.614	0.074	0.311
EP043	WC-4no.85	Landrace	Wollo	DZARC		3	0.443	0.012	0.545
EP044	WC-4no.101	Landrace	Wollo	DZARC		3	0.31	0.014	0.676
EP045	WC-5no.99	Landrace	Wollo	DZARC		3	0.004	0.016	0.98
EP046	WC-6no.50	Landrace	Wollo	DZARC		3	0.378	0.013	0.609
EP047	WC-8no.57	Landrace	Wollo	DZARC		3	0.37	0.004	0.626
EP048	WC-9no.104	Landrace	Wollo	DZARC		1	0.998	0	0.001

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP049	WC-12no.28	Landrace	Wollo	DZARC		3	0.115	0.079	0.806
EP050	WC-12no.36	Landrace	Wollo	DZARC		3	0.21	0.002	0.787
EP051	WC-12no.40	Landrace	Wollo	DZARC		3	0.203	0.002	0.795
EP052	WC-12no.53	Landrace	Wollo	DZARC		3	0.124	0.002	0.874
EP053	WC-12no.70	Landrace	Wollo	DZARC		3	0.097	0.001	0.902
EP054	WC-14no.24	Landrace	Wollo	DZARC		3	0.104	0.001	0.895
EP055	WC-14no.29	Landrace	Wollo	DZARC		3	0.137	0.001	0.862
EP056	WC-14no.53	Landrace	Wollo	DZARC		3	0.072	0.089	0.838
EP057	WC-14no.61	Landrace	Wollo	DZARC		3	0.241	0.001	0.759
EP058	WC-14no.72	Landrace	Wollo	DZARC		3	0.371	0.002	0.627
EP059	WC-15no.105	Landrace	Wollo	DZARC		3	0.175	0.001	0.824
EP060	WC-16no.57	Landrace	Wollo	DZARC		3	0.21	0.001	0.789
EP061	WC-16no.88	Landrace	Wollo	DZARC		3	0.031	0.002	0.967
EP062	DW-K-Ino.39	Landrace	DZARC(Debre Zeit)	DZARC		1	0.76	0	0.239
EP063	DW-K-Ino.42	Landrace	DZARC(Debre Zeit)	DZARC		1	0.735	0	0.265
EP064	DW-K-Ino.52	Landrace	DZARC(Debre Zeit)	DZARC		1	0.749	0	0.251
EP065	DW-K-Ino.63	Landrace	DZARC(Debre Zeit)	DZARC		1	0.749	0	0.25
EP066	DW-K-Ino.67	Landrace	DZARC(Debre Zeit)	DZARC		1	0.751	0	0.249
EP067	DW-K-Ino.128	Landrace	DZARC(Debre Zeit)	DZARC		1	0.735	0	0.265
EP068	DW-A-Ino.27	Landrace	Akaki(Shewa)	DZARC		3	0.161	0.001	0.839
EP069	DW-A-Ino.33	Landrace	Akaki(Shewa)	DZARC		3	0.156	0	0.843
EP070	DW-A-Ino.48	Landrace	Akaki(Shewa)	DZARC		3	0.156	0.001	0.844
EP071	DW-A-Ino.52	Landrace	Akaki(Shewa)	DZARC		3	0.164	0.001	0.836
EP072	DW-A-Ino.57	Landrace	Akaki(Shewa)	DZARC		3	0.153	0	0.846
EP074	DW-A-Ino.1	Landrace	Akaki(Shewa)	DZARC		3	0.317	0.039	0.644
EP075	DW-A-Ino.19	Landrace	Akaki(Shewa)	DZARC		3	0.002	0.031	0.967
EP076	DW-A-Ino.21	Landrace	Akaki(Shewa)	DZARC		1	0.453	0.38	0.167

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of released	Group	S1	S2	S3
EP077	DW-A-Ino.50	Landrace	Akaki(Shewa)	DZARC		3	0.265	0.067	0.668
EP078	DW-B-3no.22	Landrace	Gojjam(Bichena)	DZARC		3	0.323	0.034	0.643
EP079	DW-B-3no.24	Landrace	Gojjam(Bichena)	DZARC		3	0.001	0.001	0.998
EP080	DW-B-3no.30	Landrace	Gojjam(Bichena)	DZARC		3	0.001	0.001	0.998
EP081	DW-B-3no.32	Landrace	Gojjam(Bichena)	DZARC		3	0.001	0.001	0.998
EP082	DW-A-3no.38	Landrace	Akaki(Shewa)	DZARC		3	0.004	0.02	0.976
EP083	DW-A-3no.40	Landrace	Akaki(Shewa)	DZARC		3	0.298	0.022	0.68
EP084	DW-A-3no.50	Landrace	Akaki(Shewa)	DZARC		3	0.139	0.001	0.86
EP085	DW-A-3no.58	Landrace	Akaki(Shewa)	DZARC		3	0.001	0	0.999
EP086	DW-A-3no.60	Landrace	Akaki(Shewa)	DZARC		3	0.098	0.001	0.902
EP087	CD-1no.10	Landrace	USA	DZARC		3	0.184	0	0.815
EP088	CD-1no.14	Landrace	USA	DZARC		3	0.162	0.001	0.837
EP089	CD-1no.25	Landrace	USA	DZARC		3	0.323	0	0.676
EP090	CD-1no.36	Landrace	USA	DZARC		3	0.323	0	0.677
EP091	CD-1no.39	Landrace	USA	DZARC		3	0.316	0	0.684
EP092	CD-1no.55	Landrace	USA	DZARC		3	0.319	0	0.681
EP093	CD-1no.58	Landrace	USA	DZARC		3	0.235	0	0.764
EP094	CD-1no.61	Landrace	USA	DZARC		3	0.144	0.003	0.854
EP095	Gondar-19-no.33	Landrace	Gondar	DZARC		3	0.379	0.001	0.62
EP096	CD-1no.79	Landrace	USA	DZARC		3	0.125	0.001	0.875
EP097	DW-K2no.40	Landrace	DZARC(Debre Zeit)	DZARC		1	0.757	0	0.243
EP098	DW-K2no.47	Landrace	DZARC(Debre Zeit)	DZARC		1	0.762	0	0.237
EP099	DW-K2no.60	Landrace	DZARC(Debre Zeit)	DZARC		1	0.742	0	0.258
EP100	Gojam-23no.3	Landrace	Gojjam	DZARC		1	0.755	0.024	0.221
EP101	Gojam-24no.31	Landrace	Gojjam	DZARC		2	0	0.999	0
EP102	Selam	Variety	DZARC(Debre Zeit)	DZARC	2004	1	0.902	0	0.098
EP103	Asassa	Variety	DZARC(Debre Zeit)	DZARC	1997	2	0.042	0.956	0.002

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP104	Megenagna	Variety	DZARC(Debre Zeit)	DZARC	2004	2	0	0.999	0
EP105	Werer	Variety	DZARC(Debre Zeit)	DZARC	2009	2	0.001	0.999	0
EP106	Mettaya	Variety	DZARC(Debre Zeit)	DZARC	2004	2	0.001	0.998	0.001
EP107	Ejersa	Variety	SARC(Bale)	SARC	2005	2	0.001	0.998	0.001
EP108	Flakit	Variety	DZARC(Debre Zeit)	DZARC	2007	2	0	0.999	0.001
EP109	Ude	Variety	DZARC(Debre Zeit)	DZARC	2002	2	0.029	0.963	0.008
EP110	Malefia	Variety	DZARC(Debre Zeit)	DZARC	2005	2	0.113	0.845	0.041
EP111	Quamy	Variety	DZARC(Debre Zeit)	DZARC	1996	2	0.015	0.983	0.002
EP112	Mossobo	Variety	DZARC(Debre Zeit)	DZARC	2004	2	0	0.999	0
EP113	Ginchi	Variety	DZARC(Debre Zeit)	DZARC	2000	2	0.001	0.999	0.001
EP114	Toltu	Variety	SARC(Bale)	SARC	2010	2	0.001	0.999	0
EP115	Yerer	Variety	DZARC(Debre Zeit)	DZARC	2004	2	0.026	0.946	0.028
EP116	Obsa	Variety	SARC(Bale)	SARC	2006	2	0.001	0.999	0
EP117	Bichena	Variety	DZARC(Debre Zeit)	DZARC	1995	2	0	0.999	0
EP118	Leliso	Variety	SARC(Bale)	SARC	2002	2	0.001	0.999	0.001
EP119	Denbi	Variety	DZARC(Debre Zeit)	DZARC	2009	2	0.001	0.999	0
EP120	Tate	Variety	SARC(Bale)	SARC	2009	2	0	0.999	0
EP121	Hitosa	Variety	DZARC(Debre Zeit)	DZARC	2009	2	0	0.999	0
EP122	Bakalcha	Variety	SARC(Bale)	SARC	2005	2	0.003	0.996	0.001
EP123	Kilinto	Variety	DZARC(Debre Zeit)	DZARC	1994	2	0.001	0.999	0
EP124	Oda	Variety	SARC(Bale)	SARC	2004	2	0.012	0.987	0.002
EP125	Kokate	Variety	DZARC(Debre Zeit)	DZARC	2005	2	0.001	0.998	0.001
EP126	Ilani	Variety	SARC(Bale)	SARC	2004	2	0.116	0.883	0.001
EP127	2000/01population69-47FRno.75	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP128	2000/01population69-47FRno.83	Landrace	SARC(Bale)	SARC		1	0.998	0	0.001
EP129	2000/01population69-47FRno.93	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP130	2000/01population69-47FRno.95	Landrace	SARC(Bale)	SARC		1	0.997	0.001	0.002

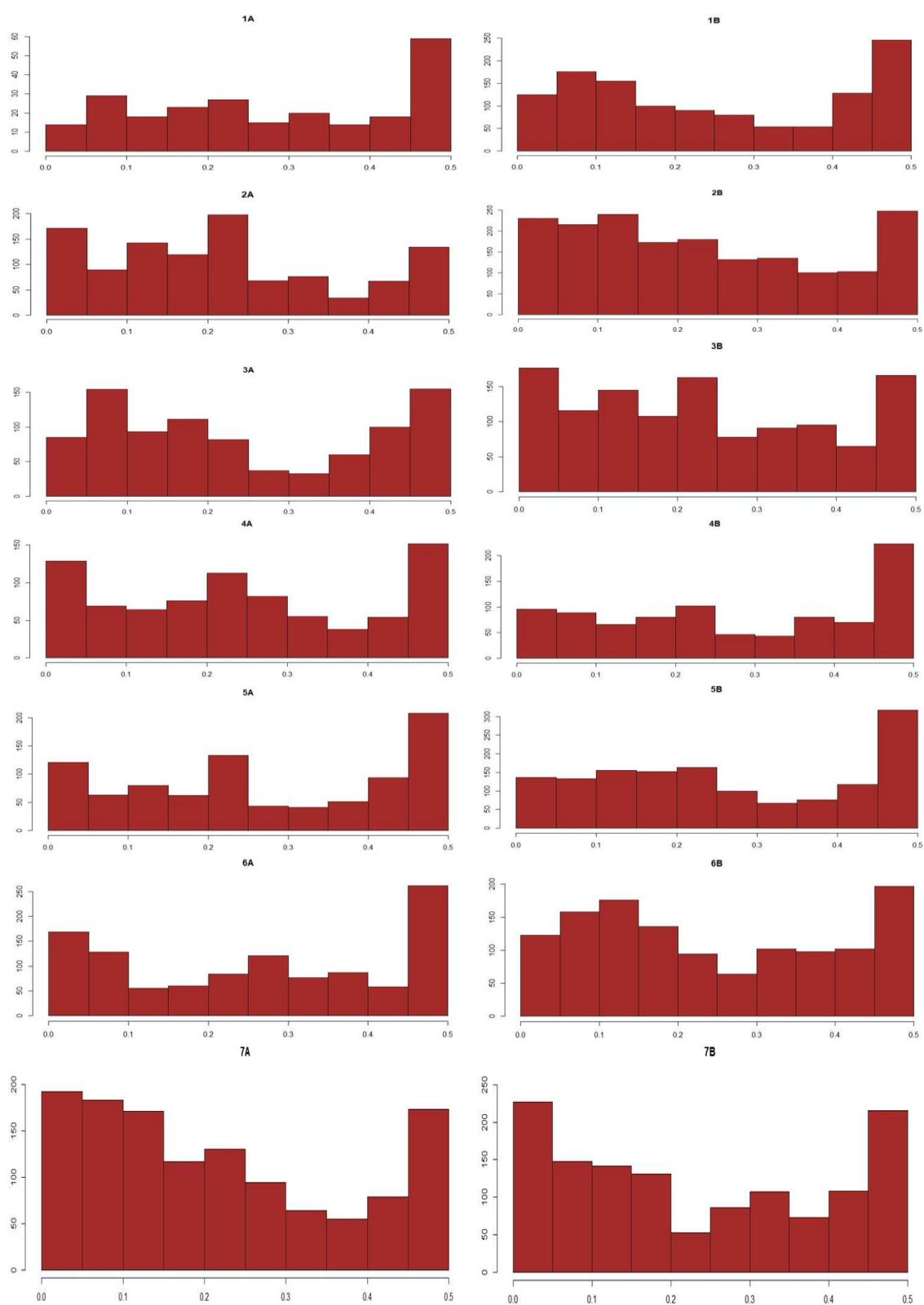
ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP131	2000/01population69-47FRno.99	Landrace	SARC(Bale)	SARC		1	0.998	0	0.001
EP132	2000/01population69-47FRno.101	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP133	2000/01population69-47FRno.102	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP134	2000/01population69-47FRno.103	Landrace	SARC(Bale)	SARC		1	0.986	0.001	0.013
EP135	2000/01populationFRno.11	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP136	2000/01populationFRno.16	Landrace	SARC(Bale)	SARC		1	0.998	0.001	0.001
EP137	2000/01populationFRno.29	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP138	2000/01populationFRno.30	Landrace	SARC(Bale)	SARC		1	0.987	0.001	0.012
EP139	2000/01populationFRno.40	Landrace	SARC(Bale)	SARC		1	0.979	0.001	0.02
EP140	2000/01populationFRno.43	Landrace	SARC(Bale)	SARC		1	0.998	0.001	0.001
EP141	2000/01populationFRno.45	Landrace	SARC(Bale)	SARC		1	0.987	0.001	0.012
EP142	2000/01populationFRno.85	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP143	2000/01populationFRno.87	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP144	2000/01populationFRno.88	Landrace	SARC(Bale)	SARC		1	0.996	0	0.004
EP145	2000/01population75-51FRno.92	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP146	2000/01population75-51FRno.15	Landrace	SARC(Bale)	SARC		1	0.997	0.003	0.001
EP147	2000/01population75-51FRno.23	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP149	2000/01population75-51FRno.41	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP150	2000/01population75-51FRno.51	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP151	2000/01population75-51FRno.57	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP152	2000/01population90FRno.59	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP153	2000/01population75-51FRno.92	Landrace	SARC(Bale)	SARC		1	0.884	0.001	0.116
EP154	2000/01population37-30BDIno.7	Landrace	SARC(Bale)	SARC		2	0.085	0.91	0.005
EP155	2000/01population37-30BDIno.10	Landrace	SARC(Bale)	SARC		1	0.999	0.001	0.001
EP156	2000/01population37-30BDIno.12	Landrace	SARC(Bale)	SARC		1	0.795	0.001	0.204
EP157	2000/01population37-30BDIno.20	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP158	2000/01population37-30BDIno.26	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001

ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP159	2000/01population37-30BDIno.36	Landrace	SARC(Bale)	SARC		3	0.082	0.019	0.898
EP160	2000/01population37-30BDIno.51	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP162	2000/01population37-30BDIno.55	Landrace	SARC(Bale)	SARC		3	0.083	0.02	0.897
EP163	2000/01population37-30BDIno.63	Landrace	SARC(Bale)	SARC		1	0.745	0.001	0.254
EP164	2000/01population37-30BDIno.105	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP165	2000/01population14no.3	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP166	2000/01population14no.5	Landrace	SARC(Bale)	SARC		1	0.751	0.007	0.242
EP167	2000/01population14no.10	Landrace	SARC(Bale)	SARC		3	0.099	0.021	0.88
EP168	2000/01population14no.13	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP169	2000/01population14no.36	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP170	2000/01population14no.45	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP171	2000/01population14no.55	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP172	2000/01population14no.60	Landrace	SARC(Bale)	SARC		1	0.999	0	0
EP173	2000/01population14no.81	Landrace	SARC(Bale)	SARC		1	0.999	0	0.001
EP174	2000/01population14no.94	Landrace	SARC(Bale)	SARC		2	0.001	0.999	0.001
EP175	2000/01population14no.106	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP176	2000/01population25-23BDIno.1	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP179	2000/01population25-23BDIno.18	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP180	2000/01population25-23BDIno.22	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP181	2000/01population25-23BDIno.24	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP182	2000/01population25-23BDIno.27	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP183	2000/01population25-23BDIno.29	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP184	2000/01population25-23BDIno.35	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP185	2000/01population25-23BDIno.42	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP186	2000/01population25-23BDIno.45	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP187	2000/01population25-23BDIno.48	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP188	2000/01population25-23BDIno.50	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999

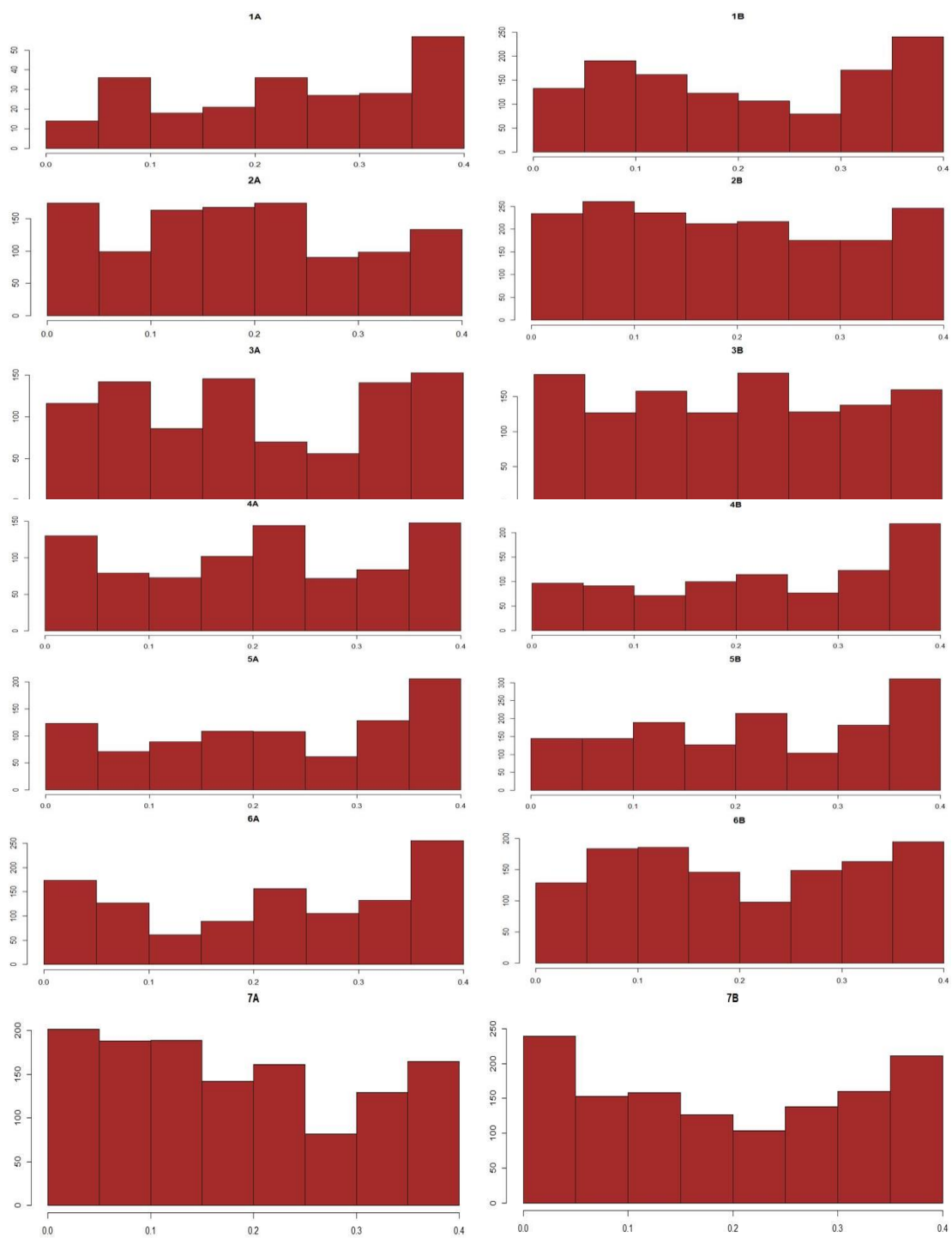
ID	Accessions name	Accession type	Cultivated area/ Released Institute	Seed source	Year of release	Group	S1	S2	S3
EP189	2000/01population25-23BDIno.57	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP190	2000/01population25-23BDIno.60	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP191	2000/01population25-23BDIno.64	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP192	2000/01population25-23BDIno.68	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP193	2000/01population25-23BDIno.72	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP194	2000/01population25-23BDIno.80	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP195	2000/01population25-23BDIno.83	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP196	2000/01population25-23BDIno.90	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP197	2000/01population25-23BDIno.93	Landrace	SARC(Bale)	SARC		3	0.001	0	0.999
EP198	2000/01population25-23BDIno.105	Landrace	SARC(Bale)	SARC		1	0.909	0.001	0.09
EP199	2000/02population82no.4	Landrace	SARC(Bale)	SARC		1	0.995	0	0.005
EP200	2000/02population82no.5	Landrace	SARC(Bale)	SARC		1	0.997	0	0.002

DZARC=Debre Zeit Agricultural Research Center; SARC=Sinana Agricultural Research Center; S1=Cluster 1;

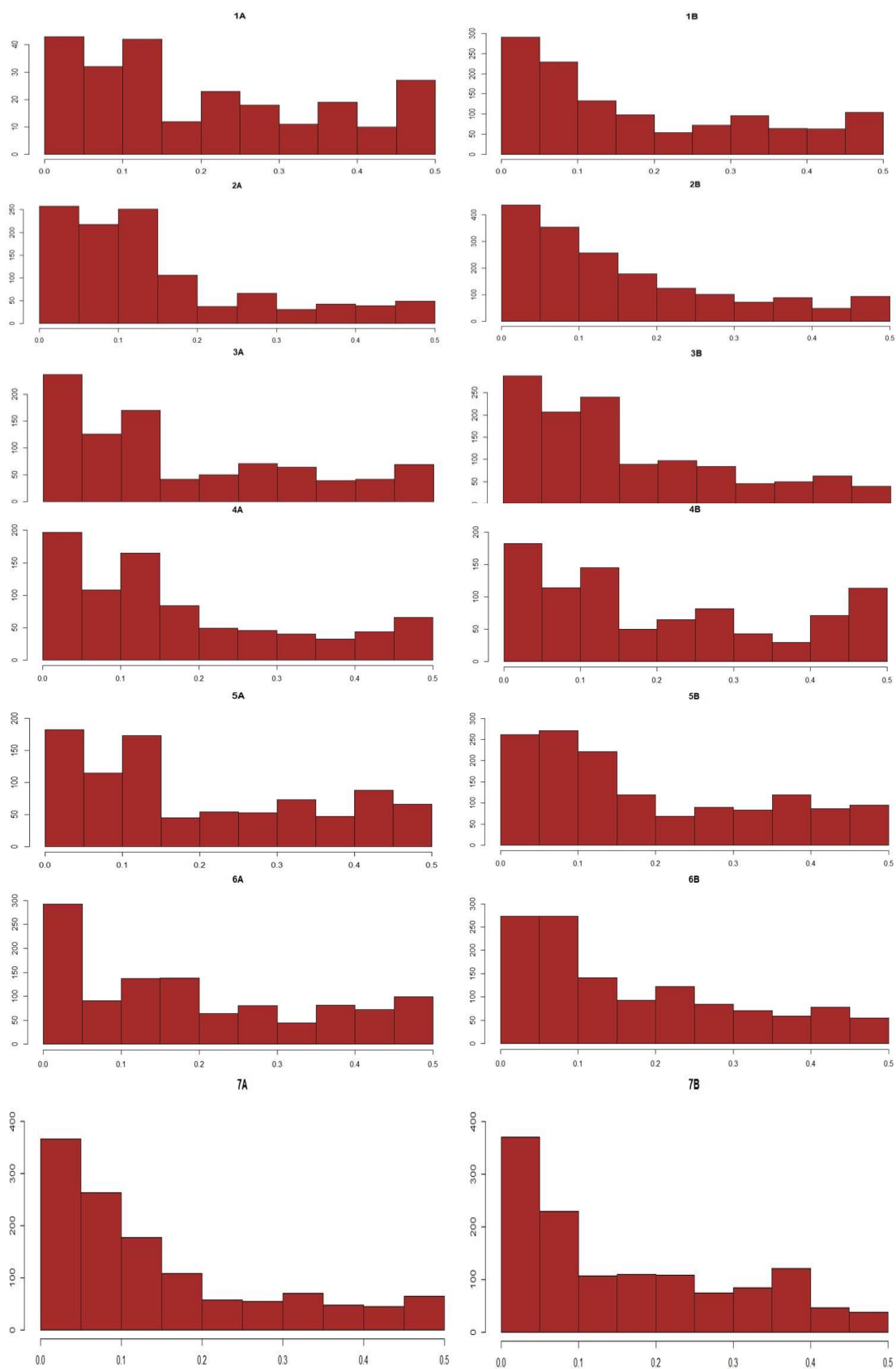
S2=Cluster 2; S3=Cluster 3



Appendix Figure 1. Frequency distributions for Nie's gene diversity score of polymorphic SNPs across chromosomes in Ethiopian durum wheat accessions.



Appendix Figure 2. Frequency distributions for polymorphic information content (PIC) values of polymorphic SNPs across chromosomes in Ethiopian durum wheat accessions.



Appendix Figure 3. Frequency distributions for minor allele frequency (MAF) values of polymorphic SNPs across chromosomes for Ethiopian durum wheat.

Appendix Table 2. Inference of the optimal numbers of clusters existed in Ethiopian durum wheat panel using Ad-hoc statistics.

K	L(K)	stdev	L'(K)	L''(K)	L''(K)	Delta K
1	-157376	3.369	-	-	-	-
2	-138930	1370.013	18446.93	-3224.75	3224.75	2.35
3	-123708	543.0884	15222.19	-5458.76	5458.76	10.05
4	-113944	1149.967	9763.425	-1419.46	1419.46	1.23
5	-105600	708.175	8343.965	-3511.28	3511.28	4.96
6	-100768	677.594	4832.685	-1326.03	1326.025	1.96
7	-97261	1353.421	3506.66	580.6019	580.6019	0.43
8	-93173	1398.676	4087.262	-1491.05	1491.054	1.07
9	-90577	1708.376	2596.208	635.7119	635.7119	0.37
10	-87345	2170.333	3231.92			

Where;

K = Subpopulations;

Ln (PD) = The log likelihood for each K;

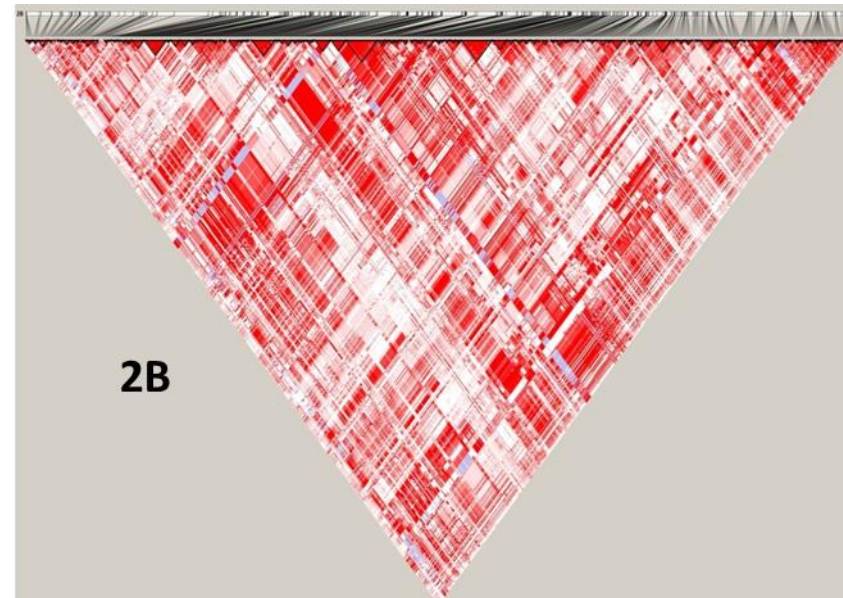
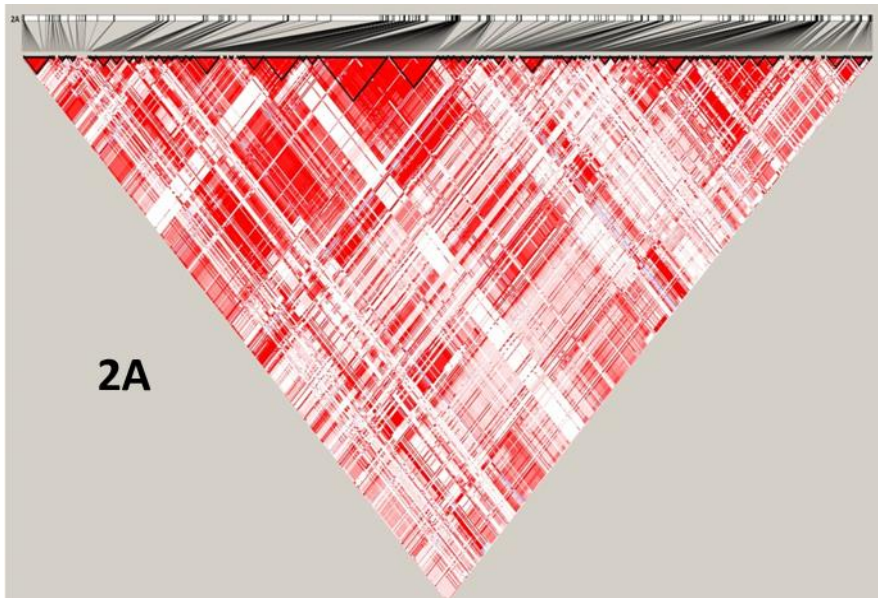
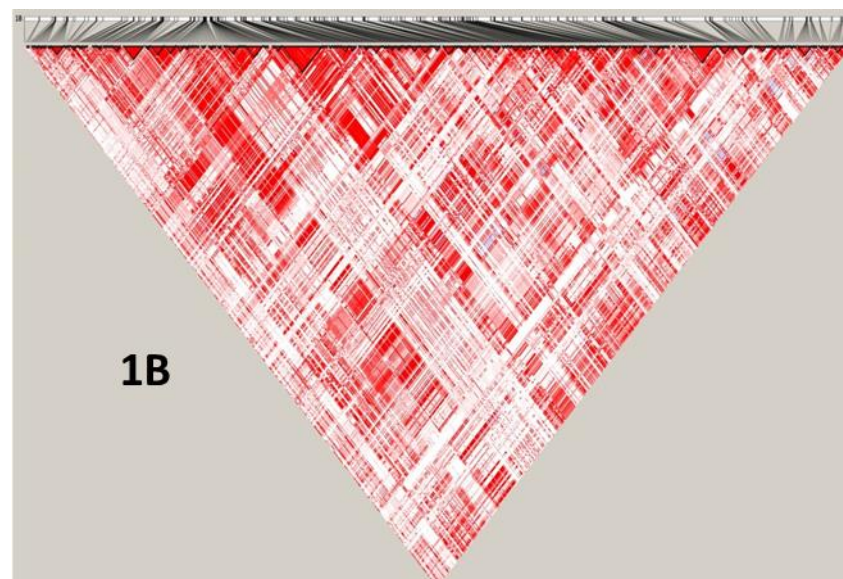
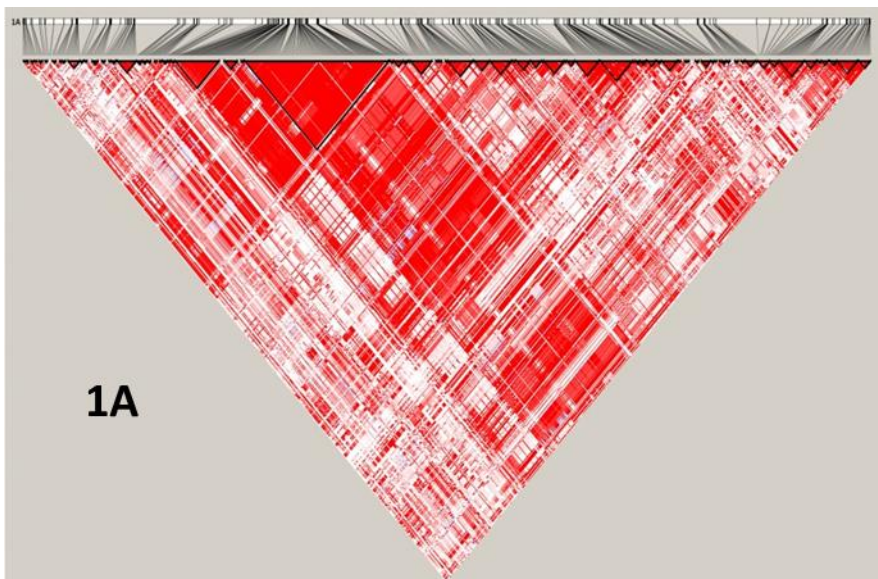
L (K) = An average of 20 values of Ln P(D);

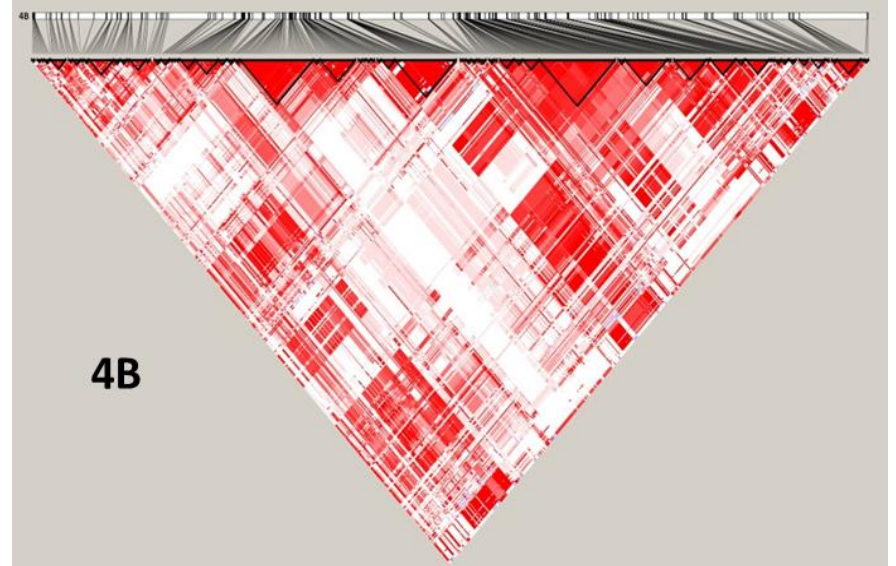
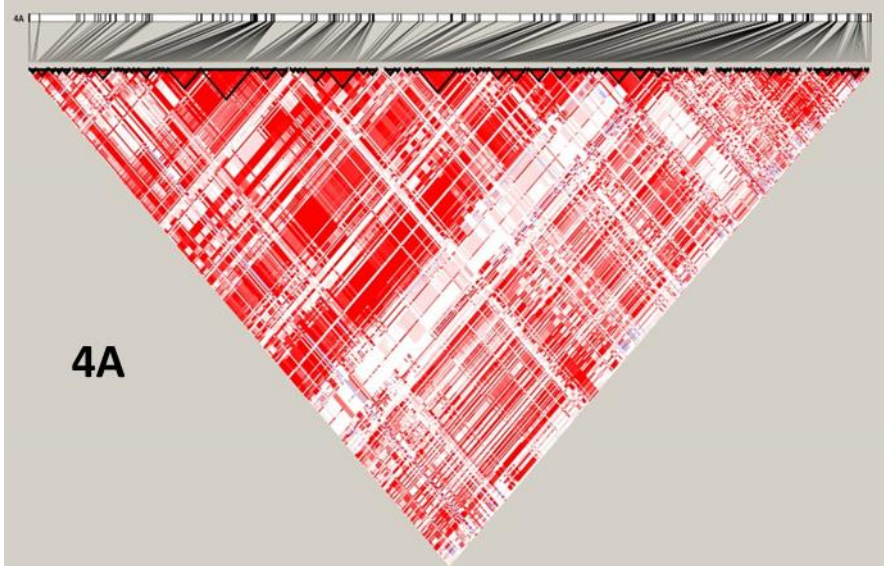
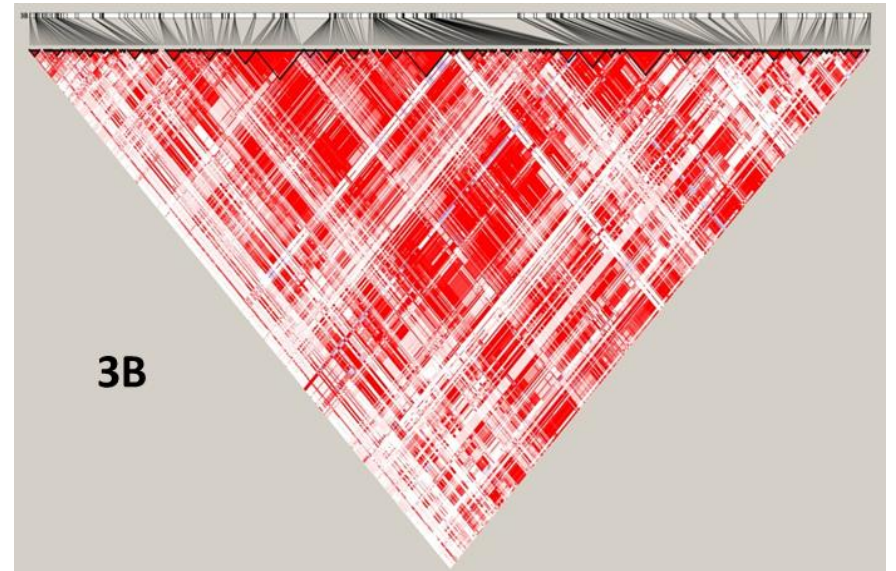
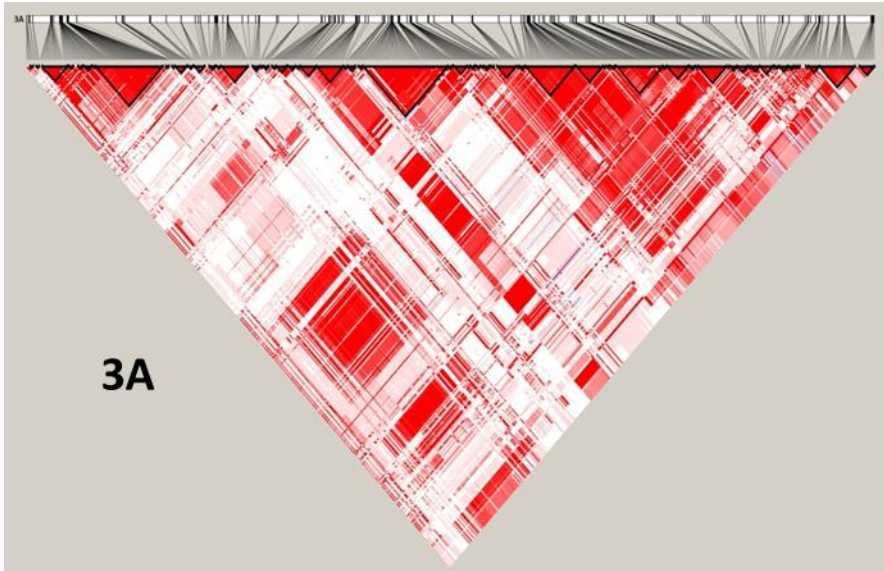
stdev = Standard deviation for 20 values of Ln P(D);

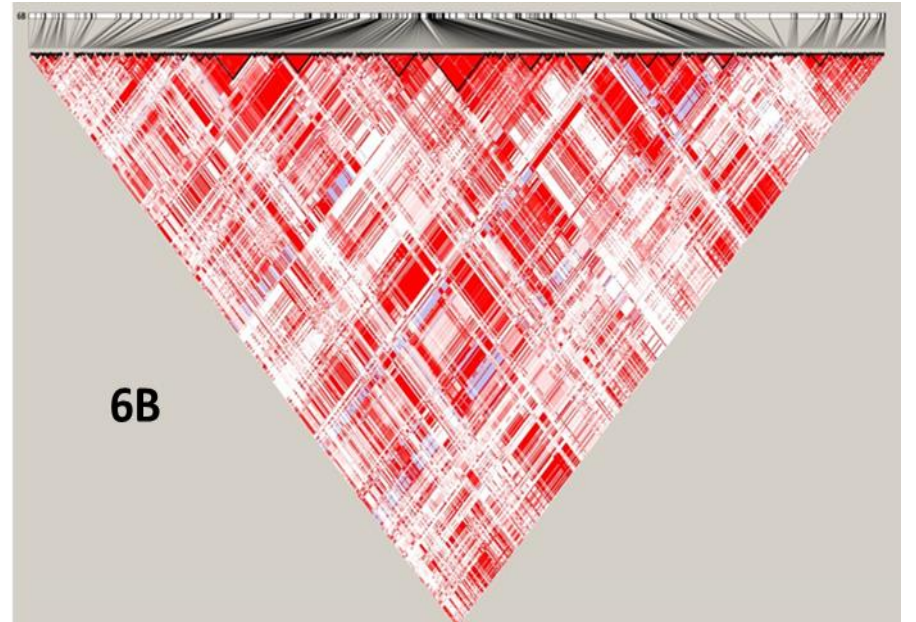
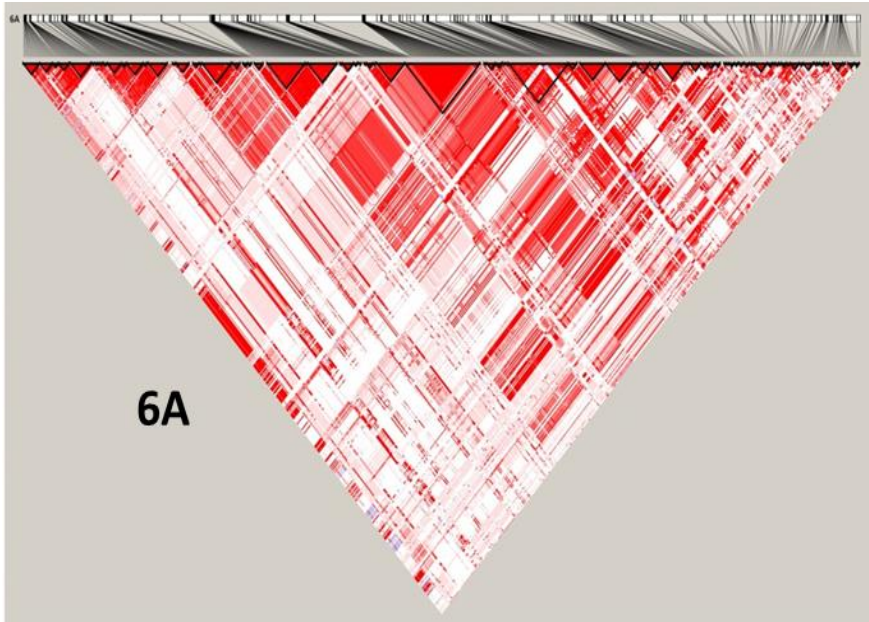
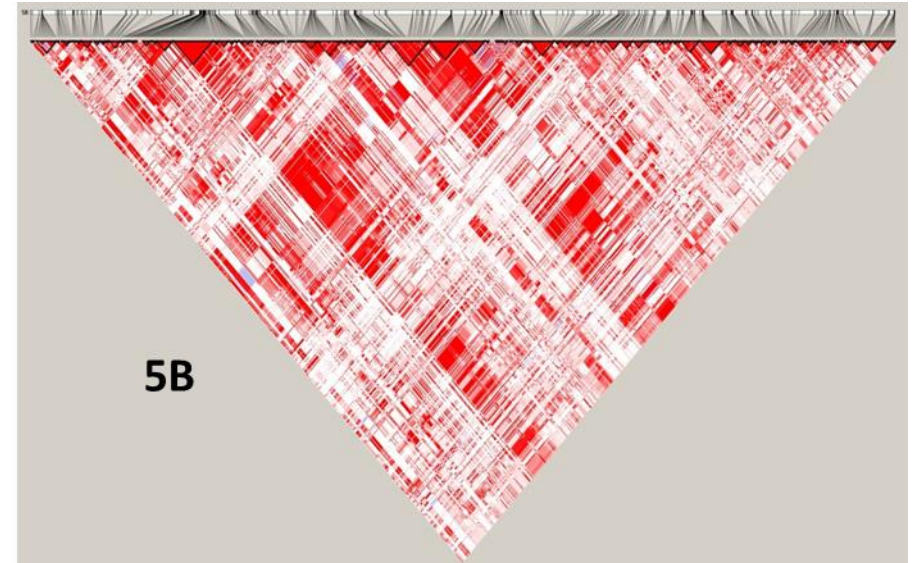
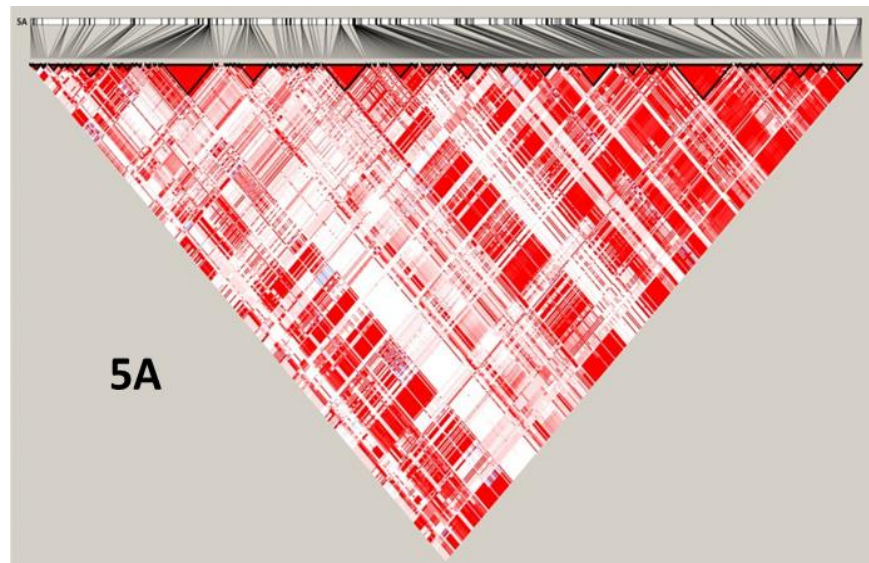
$L' (K) = L(K)_n - L(K)_{n-1}$;

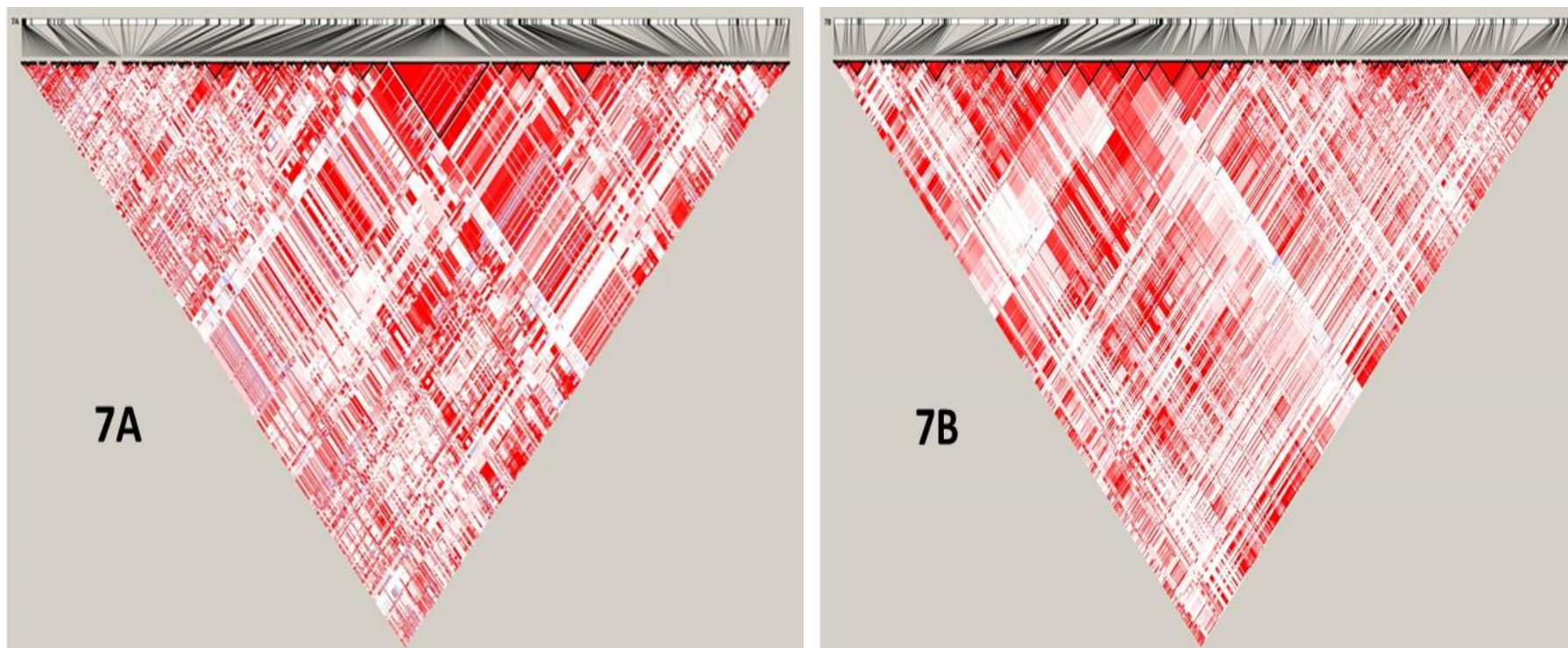
$L'' (K) = L'(K)_{n+1} - L'(K)$;

$\Delta K = |L'' (K)|/Stdev$;









Appendix Figure 4. Linkage disequilibrium plot and haplotype blocks of SNP markers in each chromosome generated from 192 Ethiopian durum wheat accessions.

Appendix Table 3. Phenotypic mean values of root system architecture (RSA) traits measured for 12-day-old seedlings in Ethiopian durum wheat accessions.

ID	iTGW	TRL	ARL	RGA	TRN	RDW	IRW	SDW	RSR	RT6
EP001	41.03	110.24	23.33	120.28	4.68	46.44	9.92	61.12	73.19	0
EP002	41.83	105.99	22.07	89.54	4.80	45.22	9.42	48.96	86.84	0.33
EP003	36.8	128.81	24.54	76.40	5.32	47.35	8.91	50.20	91.75	0.5
EP004	45.18	180.01	29.75	89.87	6.01	70.30	11.69	80.92	86.46	1
EP005	47.65	121.52	24.02	115.04	5.06	51.40	10.16	56.59	92.26	0.27
EP006	41.03	147.49	30.53	108.42	4.86	65.17	13.42	80.63	81.15	0.2
EP007	50.63	134.60	30.30	122.60	4.42	64.58	14.61	77.31	84.09	0
EP008	53.08	127.29	24.93	95.41	5.13	60.95	11.88	69.45	88.50	0.2
EP009	40.97	132.00	25.06	120.66	5.28	53.02	10.04	78.95	72.87	0.37
EP010	41.93	147.92	31.70	60.40	4.72	65.61	13.89	90.51	78.04	0.17
EP011	45.93	153.34	30.65	45.76	4.93	61.67	12.50	73.77	81.17	0.25
EP012	35.12	112.94	22.87	121.52	4.77	38.98	8.18	52.66	70.70	0.25
EP013	42.83	141.37	27.03	115.10	5.24	53.66	10.23	59.42	88.54	0.27
EP014	37.18	142.54	25.04	47.82	5.72	54.71	9.56	63.47	85.68	0.67
EP015	41.68	137.14	27.09	75.92	5.03	57.09	11.35	61.97	90.53	0.2
EP016	39.8	153.37	26.72	106.39	5.74	70.65	12.32	73.32	94.71	0.63
EP017	38.07	132.27	25.64	93.67	5.15	58.58	11.36	64.97	91.22	0.37
EP018	39.68	113.03	21.31	119.08	5.32	44.30	8.33	53.41	84.52	0.43
EP019	44.58	120.03	24.86	51.63	4.91	46.35	9.43	62.28	83.43	0.27
EP020	40.33	144.65	27.40	76.64	5.29	52.28	9.88	60.18	94.37	0.43
EP021	29.55	130.79	24.48	81.58	5.20	56.59	10.88	52.39	104.63	0.5
EP022	38.33	114.49	21.63	87.87	5.40	42.55	7.88	44.96	88.10	0.43
EP023	38.22	111.38	23.93	103.29	4.65	52.51	11.30	62.48	83.33	0.17
EP024	48.73	120.31	22.88	102.56	5.18	58.96	11.39	69.26	84.66	0.37
EP025	47.37	115.14	23.76	106.93	4.88	46.29	9.49	50.26	91.73	0.33
EP026	42.27	66.26	16.58	96.40	4.10	38.77	9.47	44.11	85.41	0
EP028	41.45	88.52	24.33	103.08	3.66	38.95	10.63	46.11	85.03	0
EP029	53.67	141.03	26.43	112.93	5.31	49.35	9.29	65.61	83.40	0.33
EP030	36.88	146.98	27.97	83.60	5.39	53.61	9.94	64.84	89.50	0.6
EP031	48.75	114.51	21.24	119.43	5.35	51.95	9.71	64.71	75.64	0.5

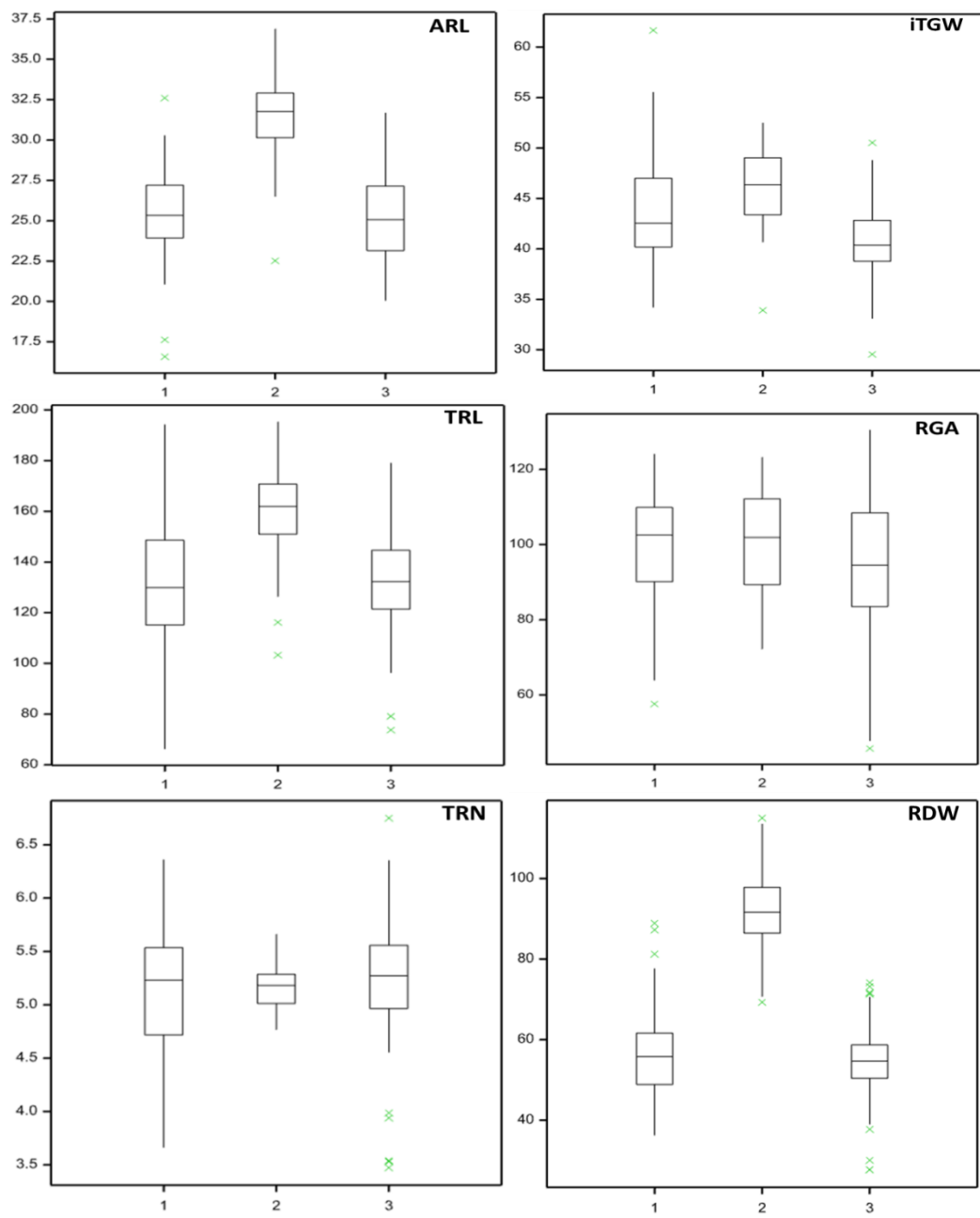
ID	ITGW	TRL	ARL	RGA	TRN	RDW	IRW	SDW	RSR	RT6
EP032	39.58	120.76	21.90	113.87	5.47	52.22	9.55	56.63	86.87	0.77
EP033	41.87	150.18	22.54	110.47	6.75	64.01	9.48	71.53	87.45	1
EP034	42.22	150.19	24.78	63.93	6.07	53.67	8.85	62.53	84.80	0.9
EP036	39.53	136.39	25.82	59.11	5.39	50.40	9.35	55.93	90.13	0.63
EP037	37.43	125.55	25.89	102.18	4.89	47.84	9.78	52.63	90.42	0.17
EP038	41.33	142.03	27.79	83.50	5.22	66.24	12.69	85.97	77.36	0.47
EP039	39.75	121.42	23.19	87.01	5.26	51.62	9.81	64.11	80.93	0.5
EP041	34.37	117.77	21.41	71.95	5.53	46.94	8.48	50.65	87.01	0.5
EP042	38.97	82.58	17.63	57.61	4.59	41.47	9.04	46.99	81.92	0
EP043	34.3	154.16	30.57	98.83	4.98	56.09	11.27	60.12	92.27	0.25
EP044	39.85	145.90	26.21	62.59	5.56	58.71	10.57	76.81	75.51	0.65
EP045	33.4	97.92	25.05	95.68	3.94	50.26	12.76	60.88	82.20	0.43
EP046	39.05	154.92	24.66	113.12	6.36	73.17	11.51	91.96	79.38	0.93
EP047	41.32	142.20	25.80	104.80	5.49	64.91	11.83	74.64	87.46	0.63
EP048	34.2	108.59	22.96	103.14	4.56	36.28	7.95	40.78	90.43	0
EP049	34.42	142.90	26.06	83.46	6.08	47.35	7.79	63.61	82.27	0.75
EP050	44.68	157.95	29.04	115.84	5.42	59.61	10.99	75.18	85.54	0.5
EP051	45.18	125.43	22.27	101.62	5.68	61.37	10.80	73.21	83.44	0.3
EP052	39.43	104.32	23.09	122.43	4.55	43.71	9.60	57.32	72.79	0.15
EP053	38.78	138.34	24.41	123.52	5.66	62.22	10.99	72.69	85.10	0.6
EP054	41.93	139.11	28.79	120.37	4.78	55.96	11.71	65.59	84.46	0.27
EP055	45.83	140.36	28.59	121.00	4.96	58.69	11.82	58.69	101.01	0.4
EP056	37.52	134.76	27.14	129.59	4.96	56.93	11.49	57.61	99.65	0.3
EP057	39.37	145.59	26.47	90.84	5.56	63.46	11.42	76.78	83.31	0.7
EP058	37.65	115.73	25.01	111.55	4.65	43.64	9.38	48.41	91.95	0
EP059	35.32	79.18	23.01	109.15	3.47	27.75	7.99	46.31	71.70	0
EP060	33.1	96.49	20.29	110.89	4.66	27.71	5.94	36.92	90.73	0.33
EP061	40.42	127.78	22.07	130.53	5.75	53.62	9.33	50.71	99.54	0.73
EP062	41.82	95.14	22.12	85.22	4.27	42.48	9.96	50.16	81.05	0
EP063	38.43	107.88	23.37	115.90	4.55	46.68	10.26	54.20	82.52	0.17
EP064	40.17	103.84	23.08	86.50	4.51	44.50	9.87	46.68	92.39	0
EP065	43.07	127.29	26.36	109.73	4.80	61.36	12.79	72.69	83.61	0.15
EP066	41.62	107.50	27.02	121.33	3.91	55.79	14.28	64.63	85.45	0

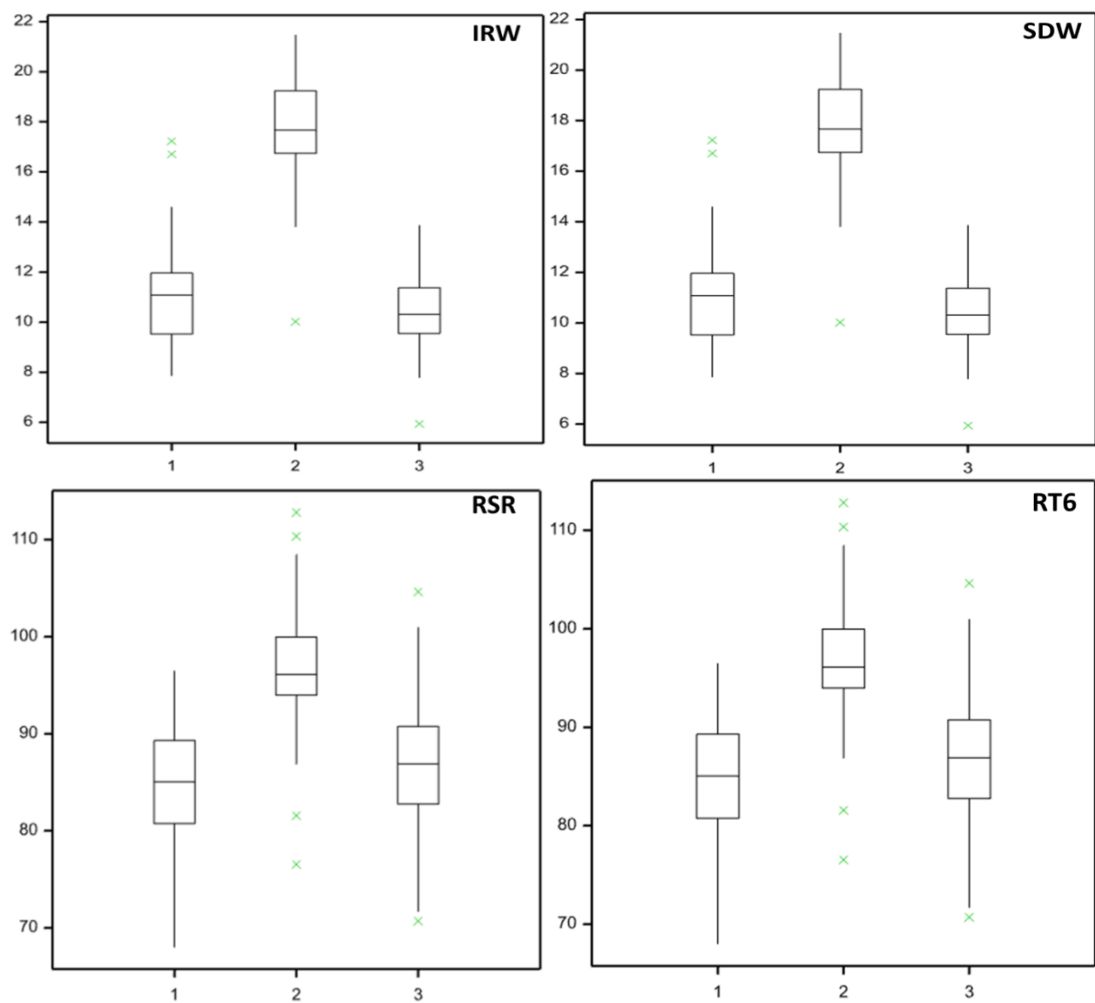
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EP067	41.03	121.29	24.70	114.54	4.86	57.13	11.76	64.11	89.24	0.27
EP068	44.2	141.22	27.93	66.84	5.00	54.62	10.93	58.45	94.40	0.17
EP069	43.02	100.88	26.14	68.99	3.99	46.79	11.74	58.59	88.45	0
EP070	42.83	133.18	29.34	66.64	4.56	52.94	11.61	66.51	86.97	0.17
EP071	42.95	141.13	27.02	107.55	5.15	58.21	11.29	68.24	81.04	0.17
EP072	45.43	109.54	22.92	90.75	4.97	52.31	10.52	60.03	85.05	0.15
EP074	42.22	112.25	22.32	57.87	4.95	50.63	10.24	55.26	91.49	0.2
EP075	39.58	151.52	26.03	87.60	5.90	61.02	10.35	69.69	86.61	0.83
EP076	45.45	113.22	24.23	90.95	4.59	50.84	11.08	55.29	91.42	0
EP077	33.47	175.93	30.40	51.26	5.79	74.13	12.80	81.44	91.41	0.77
EP078	39.02	168.62	28.86	105.14	5.83	49.95	8.57	56.78	88.23	0.5
EP079	38.42	142.41	27.17	83.25	5.24	51.09	9.75	67.97	83.13	0.5
EP080	40.88	148.49	28.42	81.57	5.20	54.90	10.56	69.36	84.59	0.47
EP081	50.53	140.18	25.17	121.97	5.61	71.29	12.70	76.37	89.94	0.7
EP082	42.28	150.26	27.67	101.08	5.51	56.67	10.28	61.09	89.62	0.43
EP083	39.25	152.10	27.93	94.57	5.41	54.66	10.10	66.75	80.51	0.43
EP084	46.67	122.49	25.44	86.45	4.79	51.71	10.80	55.14	92.61	0.17
EP085	41.7	129.60	24.02	93.71	5.39	47.68	8.85	54.43	86.64	0.4
EP086	39.77	131.75	25.79	95.45	5.16	57.17	11.09	77.29	73.62	0.27
EP087	40.67	73.71	20.48	61.39	3.53	30.06	8.51	34.76	86.97	0
EP088	47.62	124.79	23.39	76.38	5.33	62.95	11.81	76.45	83.00	0.4
EP089	45.65	79.11	23.31	92.05	3.54	37.75	10.66	47.97	90.37	0
EP090	47.47	150.91	27.90	118.20	5.40	51.17	9.47	66.43	83.26	0.35
EP091	43.58	99.61	20.60	102.00	4.78	48.29	10.10	50.04	90.74	0.1
EP092	43.55	131.99	23.83	108.89	5.61	58.67	10.45	61.75	91.48	0.67
EP093	41.4	123.51	25.07	108.27	4.92	49.01	9.97	57.20	82.75	0.17
EP094	38.93	151.95	27.55	85.67	5.68	71.63	12.61	89.59	79.33	0.53
EP095	36.63	142.46	25.69	68.00	5.60	71.69	12.81	84.69	83.81	0.6
EP096	40.3	140.25	27.89	83.68	4.99	48.17	9.66	53.96	88.48	0.33
EP097	37.88	164.13	29.40	78.20	5.56	72.13	12.98	79.11	91.74	0.63
EP098	44.87	147.36	26.99	97.11	5.53	73.28	13.25	86.78	85.26	0.47
EP099	42.18	142.86	27.79	111.23	5.18	61.69	11.91	87.95	74.96	0.27
EP100	45.55	151.85	30.29	116.14	5.06	87.24	17.23	92.69	96.29	0.17

ID	ITGW	TRL	ARL	RGA	TRN	RDW	IRW	SDW	RSR	RT6
EP101	43.32	155.96	30.17	115.31	5.24	100.55	19.21	102.29	96.10	0.33
EP102	45.35	117.94	26.02	124.17	4.69	53.07	11.31	65.22	78.69	0.1
EP103	45.35	161.95	32.87	113.24	4.91	98.24	20.00	102.34	94.94	0.1
EP104	33.92	145.85	28.52	123.35	5.11	88.92	17.39	91.53	95.75	0.33
EP105	49.07	103.29	27.89	104.00	3.73	52.02	13.94	66.69	76.54	0
EP106	43.68	146.27	30.14	107.80	4.85	85.58	17.63	76.31	112.82	0.1
EP107	47.1	151.05	29.64	88.19	5.11	92.76	18.15	93.82	99.52	0.3
EP108	46.72	171.55	32.92	79.11	5.28	75.96	14.39	71.63	110.35	0.5
EP109	45.8	195.46	35.76	80.53	5.55	95.02	17.13	90.95	108.50	0.7
EP110	47.03	162.02	31.72	72.20	5.10	101.90	19.99	103.69	100.12	0.7
EP111	46.3	147.91	28.54	97.73	5.18	90.62	17.49	88.71	100.31	0.17
EP112	47.48	126.33	26.50	94.42	4.91	91.01	18.52	92.42	96.62	0.2
EP113	41.82	150.96	31.75	92.84	4.77	90.51	18.99	95.32	94.07	0
EP114	50.2	168.15	31.89	116.34	5.21	100.30	19.24	102.59	96.89	0.3
EP115	42.15	176.22	32.88	107.96	5.40	115.02	21.31	116.69	97.81	0.47
EP116	52.12	194.30	36.90	108.84	5.29	113.58	21.48	115.97	98.09	0.4
EP117	48.92	168.95	32.67	92.97	5.19	91.46	17.62	96.78	95.17	0.37
EP118	41.05	184.45	33.76	83.57	5.48	91.63	16.72	96.63	97.55	0.5
EP119	44.5	157.23	33.13	103.76	4.81	93.35	19.40	91.28	106.63	0.15
EP120	41.92	191.49	33.82	99.60	5.66	110.24	19.46	104.69	107.52	0.7
EP121	46.37	164.51	33.34	117.17	5.01	80.62	16.08	82.37	94.01	0
EP122	49.07	158.80	31.77	99.56	5.09	91.61	18.01	95.61	93.48	0.15
EP123	47.43	159.59	30.16	117.74	5.30	89.18	16.82	95.65	92.30	0.3
EP124	50.85	152.61	30.45	101.91	5.01	69.30	13.83	78.59	87.59	0.1
EP125	52.52	166.72	31.13	119.40	5.43	96.36	17.74	101.69	93.97	0.57
EP126	40.68	171.33	32.87	84.47	5.22	92.24	17.67	96.97	95.52	0.33
EP127	43.2	153.03	27.54	71.17	5.56	61.13	11.00	73.78	83.41	0.43
EP128	40.08	134.41	24.12	76.01	5.61	55.63	9.91	77.29	77.65	0.67
EP129	36.95	144.63	27.33	91.23	5.31	60.02	11.30	70.95	91.27	0.33
EP130	39.38	171.55	28.09	86.77	6.10	88.90	14.58	100.36	90.89	0.93
EP131	39.9	135.88	24.84	95.77	5.45	69.95	12.84	80.71	83.71	0.43
EP132	36.83	111.63	21.47	94.26	5.28	45.01	8.52	63.75	67.98	0.33
EP133	40.88	149.69	25.26	85.51	5.93	58.51	9.86	74.65	77.40	0.83

ID	ITGW	TRL	ARL	RGA	TRN	RDW	IRW	SDW	RSR	RT6
EP134	45.07	143.26	27.09	97.63	5.23	60.18	11.50	72.65	81.54	0.5
EP135	44.85	122.66	28.76	100.03	4.33	72.36	16.71	83.69	85.17	0.07
EP136	42.63	119.60	27.67	84.10	4.32	49.91	11.55	61.31	81.96	0.1
EP137	38.65	139.63	27.57	80.54	5.02	60.46	12.03	70.78	85.87	0.1
EP138	40.75	121.61	24.36	110.37	5.08	52.30	10.29	70.96	78.62	0.2
EP139	40.85	157.33	29.83	106.43	5.28	72.69	13.77	90.61	84.63	0.3
EP140	42.25	134.62	26.79	109.36	5.03	60.24	11.98	70.69	89.32	0.23
EP141	38.68	127.98	27.24	103.30	4.68	55.29	11.81	64.04	81.54	0
EP142	44.63	123.44	22.72	104.83	5.59	52.74	9.43	59.56	85.52	0.63
EP143	40.18	139.26	25.33	109.08	5.53	68.84	12.44	83.98	80.94	0.53
EP144	45.38	125.91	25.99	109.94	4.85	57.30	11.83	74.26	76.53	0
EP145	45.52	124.22	26.66	105.30	4.70	53.69	11.43	67.36	79.14	0
EP146	36.77	114.10	25.04	98.04	4.55	53.24	11.69	67.31	79.62	0
EP147	44.77	113.91	23.73	108.59	4.78	37.56	7.86	40.76	92.42	0
EP149	42.1	128.00	24.76	111.23	5.21	48.69	9.34	62.95	85.03	0.2
EP150	45.9	129.35	24.56	86.30	5.23	42.90	8.20	59.36	76.62	0.1
EP151	48.77	140.23	26.53	123.76	5.24	56.20	10.73	62.67	86.34	0.25
EP152	55.22	143.14	25.32	106.20	5.73	75.41	13.17	82.22	89.79	0.73
EP153	41.53	151.30	28.16	112.29	5.33	59.13	11.08	73.25	77.90	0
EP154	50.6	116.18	22.52	82.74	5.20	52.13	10.02	63.42	81.56	0.33
EP155	43.88	138.69	25.96	99.30	5.40	77.69	14.39	86.36	89.57	0.43
EP156	50.22	194.40	32.60	94.40	5.99	81.24	13.57	94.31	86.32	0.87
EP157	42.55	153.92	24.49	110.01	6.36	57.28	9.00	71.78	80.66	0.9
EP158	40.38	119.78	22.52	101.37	5.28	47.63	9.02	67.29	75.91	0
EP159	45.03	151.53	29.46	102.90	5.25	55.35	10.55	71.61	83.77	0.37
EP160	41.67	150.25	25.32	102.64	5.96	52.57	8.82	70.02	79.05	0.5
EP162	38.27	146.71	25.90	106.13	5.68	64.62	11.37	78.37	79.51	0.67
EP163	55.57	152.96	26.63	105.58	5.85	64.34	11.00	81.75	77.45	0.73
EP164	50.4	168.59	26.66	102.51	6.33	74.51	11.76	93.65	77.77	1
EP165	44.52	149.02	24.65	108.01	6.12	67.73	11.06	78.26	85.86	1
EP166	40.2	115.22	24.26	76.33	4.80	59.69	12.44	69.36	84.97	0
EP167	48.82	179.20	31.24	94.44	5.75	63.58	11.05	76.31	84.62	0.77
EP168	50.62	156.46	26.03	110.68	6.00	60.62	10.11	64.11	95.40	0.77

ID	iTGW	TRL	ARL	RGA	TRN	RDW	IRW	SDW	RSR	RT6
EP169	51.92	149.08	26.26	98.27	5.75	55.30	9.62	64.63	91.38	0.67
EP170	52.43	161.58	29.07	78.47	5.59	56.61	10.12	62.84	96.54	0.8
EP171	54.53	151.04	29.17	115.07	5.21	58.95	11.31	62.37	90.44	0.27
EP172	45.65	129.87	23.94	102.58	5.50	51.71	9.39	67.32	74.09	0.55
EP173	48.25	142.99	26.33	95.24	5.47	74.18	13.57	81.32	88.54	0.53
EP174	43.57	161.92	32.15	104.07	5.12	70.73	13.80	79.59	86.86	0.33
EP175	42.8	129.06	26.29	91.50	4.96	56.69	11.42	69.36	81.10	0.27
EP176	39.88	135.50	26.17	92.24	5.19	59.58	11.48	66.64	91.02	0.2
EP179	41.23	147.42	24.80	101.77	5.92	55.28	9.33	69.18	85.97	1
EP180	42.85	133.05	23.19	90.90	5.70	58.24	10.22	67.02	91.65	0.67
EP181	38.2	128.62	22.61	111.87	5.66	53.14	9.39	61.43	82.13	0.67
EP182	38.87	109.67	20.68	93.47	5.39	44.07	8.17	47.56	88.39	0
EP183	41.65	105.86	21.76	93.64	4.83	43.51	9.00	54.65	77.70	0.33
EP184	40.12	124.15	23.15	94.34	5.36	58.40	10.90	65.26	88.33	0.3
EP185	36.73	127.22	24.39	88.06	5.30	53.36	10.07	58.69	89.84	0.43
EP186	41.1	137.47	25.30	87.84	5.42	58.58	10.81	62.31	95.49	0.43
EP187	36.68	126.36	24.19	93.74	5.26	51.62	9.81	54.78	95.70	0.17
EP188	40.4	96.30	20.06	77.74	4.91	44.63	9.08	60.96	79.02	0.27
EP189	37.65	132.22	23.67	106.17	5.59	55.28	9.89	71.51	82.76	0.67
EP190	38.67	102.42	20.46	102.14	5.03	46.24	9.19	59.36	83.82	0.4
EP191	39.77	123.21	23.25	106.27	5.33	54.61	10.25	59.29	88.54	0.43
EP192	42.2	116.54	21.85	97.50	5.46	55.07	10.09	58.89	90.72	0.5
EP193	38.73	128.43	22.09	96.44	5.77	52.51	9.10	59.65	86.90	0.9
EP194	39.62	104.75	20.75	92.33	5.12	53.73	10.49	54.26	98.43	0.17
EP195	39.03	114.02	20.94	98.17	5.44	54.34	9.98	54.50	98.21	0.43
EP196	44.37	129.80	25.44	105.14	5.09	64.91	12.76	75.31	87.56	0.27
EP197	45.88	127.99	23.63	92.34	5.43	53.28	9.81	60.11	89.50	0.5
EP198	49.38	105.78	21.06	116.37	5.08	46.96	9.24	58.96	86.28	0.1
EP199	52.98	131.32	28.10	109.80	4.69	53.94	11.50	66.18	88.20	0
EP200	61.67	140.35	25.69	108.90	5.46	69.90	12.79	76.02	94.95	0.65





Appendix Figure 5. Box plot of the three STRUCTURE-inferred sub-populations for the mean values of RSA traits.

Appendix Table 4. List of all identified QTLs for root system architecture (RSA) traits in Ethiopian durum wheat.

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
ARL	IWB9746	1A	109.9	2.87	5.408	107.65	112.15	A	-2.29	62	C	0	130
ARL	IWA2994	1A	136.11	2.45	4.47	133.86	138.36	A	-3.39	179	G	0	13
ARL	IWB31719	1A	139.9	2.04	3.551	137.65	142.15	G	3.24	18	T	0	174
ARL	IWB164	1B	85.51	2.27	4.067	83.26	87.76	A	-2.92	26	G	0	166
ARL	IWB48378	1B	162.11	2.17	3.834	159.86	164.36	C	-2.97	36	T	0	156
ARL	IWB53380	2A	35.63	3.00	5.716	33.38	37.88	A	4.76	159	G	0	33
ARL	IWB30420	2B	174.3	2.77	5.188	172.05	176.55	A	-4.00	34	G	0	158
ARL	IWB38326	3A	136.3	2.32	4.165	134.05	138.55	A	3.48	20	C	0	172
ARL	IWB7306	3A	141.51	2.17	3.834	139.26	143.76	A	-3.18	171	G	0	21
ARL	IWB57554	3B	2.83	2.16	3.811	0.58	5.08	A	3.07	182	G	0	10
ARL	IWA3304	3B	100.58	2.05	3.576	98.33	102.83	C	2.02	178	T	0	14
ARL	IWB11967	5A	85.61	2.38	4.311	83.36	87.86	A	-2.73	176	G	0	16
ARL	IWB53060	5A	153.64	2.75	5.142	151.39	155.89	G	4.15	158	T	0	34
ARL	IWB8292	5A	156.51	2.23	3.961	154.26	158.76	A	-2.17	48	G	0	144
ARL	IWB68337	5A	173.72	2.17	3.832	171.47	175.97	A	-1.54	157	G	0	35
ARL	IWB34332	5B	120.14	2.45	4.458	117.89	122.39	A	2.17	72	G	0	120
ARL	IWB49617	5B	155.69	2.42	4.392	153.44	157.94	C	2.60	26	T	0	166
ARL	IWB23813	5B	166.14	2.95	5.32	163.89	168.39	C	-1.85	80	T	0	112
ARL	IWB47364	5B	181.92	2.61	4.823	179.67	184.17	A	2.71	175	G	0	17
ARL	IWB51018	6A	52.83	2.09	3.655	50.36	52.61	A	-3.69	30	G	0	162
ARL	IWB45612	6B	55.54	2.02	3.499	53.29	57.79	G	-3.26	148	T	0	44
ARL	IWB8871	6B	74.94	2.75	5.145	72.69	77.19	A	2.36	161	C	0	31
ARL	IWB61166	6B	94.57	2.10	3.672	92.32	96.82	A	2.31	16	G	0	176
ARL	IWB47901	7A	14.22	2.12	3.734	11.97	16.47	A	1.53	115	G	0	77

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
ARL	IWB8142	7A	87.71	2.06	3.604	85.46	89.96	A	-2.00	77	G	0	115
ARL	IWB7926	7A	91.22	2.20	3.897	88.97	93.47	A	1.52	137	G	0	55
ARL	IWB11841	7A	94.72	2.38	4.295	92.47	96.97	C	-1.61	66	T	0	126
ARL	IWB8935	7A	126	2.07	3.61	123.75	128.25	C	-1.84	101	T	0	91
ARL	IWB72331	7B	93.09	2.49	4.554	90.84	95.34	C	1.79	71	T	0	121
ARL	IWB48843	7B	138.57	2.42	4.402	136.32	140.82	C	-2.41	142	T	0	50
IRW	IWB47703	1A	122.75	2.52	4.51	120.5	125	C	-1.52	54	T	0	138
IRW	IWB60732	1B	33.75	3.10	5.803	31.5	36	A	1.70	41	G	0	151
IRW	IWB68867	1B	67.47	2.20	3.798	65.22	69.72	A	2.26	178	G	0	14
IRW	IWB56695	1B	77.32	2.18	3.75	75.07	79.57	C	-1.49	68	T	0	124
IRW	IWB36732	1B	115.42	2.13	3.653	113.17	117.67	C	2.14	15	T	0	177
IRW	IWB66543	1B	141.31	2.38	4.187	139.06	143.56	C	1.43	120	T	0	72
IRW	IWB53380	2A	35.63	2.03	3.439	33.38	37.88	A	3.09	159	G	0	33
IRW	IWB62562	2A	156.33	2.23	3.87	154.08	158.58	C	2.31	15	T	0	177
IRW	IWB66885	2B	75.45	2.03	3.436	73.2	77.7	C	-2.79	170	T	0	22
IRW	IWB5627	2B	140.42	2.27	3.948	138.17	142.67	A	0.85	105	G	0	87
IRW	IWB29332	2B	160.51	3.48	6.675	158.26	162.76	A	4.50	24	G	0	168
IRW	IWB41547	2B	181.76	2.18	3.754	179.51	184.01	A	-2.44	179	G	0	13
IRW	IWB7614	3A	79.54	2.69	4.88	77.29	81.79	C	2.01	176	T	0	16
IRW	IWB25948	3A	96.93	2.06	3.494	94.68	99.18	C	-2.52	170	T	0	22
IRW	IWB35437	3B	41.34	2.15	3.703	39.09	43.59	C	-2.35	36	T	0	156
IRW	IWA1863	3B	64.65	2.39	4.206	62.4	66.9	C	-1.28	136	C	0	56
IRW	IWB35514	3B	209.14	2.34	4.107	206.89	211.39	G	1.72	178	T	0	14
IRW	IWB56116	4A	107.2	2.20	3.808	104.95	109.45	A	3.31	28	G	0	164
IRW	IWB23476	4B	114.43	2.43	4.302	112.18	116.68	A	2.25	154	C	0	38
IRW	IWA3196	5A	16.83	4.06	8.03	14.58	19.08	C	7.54	26	T	0	166

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
IRW	IWB3232	5A	183.21	2.10	3.581	180.96	185.46	A	4.55	27	G	0	165
IRW	IWB56643	5A	210.32	2.35	4.123	208.07	212.57	C	-2.45	18	T	0	174
IRW	IWA332	5B	16.73	3.00	5.563	14.48	18.98	G	-2.96	15	T	0	177
IRW	IWB25204	5B	34.21	2.03	3.442	31.96	36.46	C	-2.02	179	T	0	13
IRW	IWB70122	5B	40.39	3.15	5.919	38.14	42.64	A	2.81	16	C	0	176
IRW	IWB72874	6A	102.6	2.06	3.513	100.35	104.85	A	-2.36	17	G	0	175
IRW	IWB6978	6B	69.32	2.09	3.572	67.07	71.57	C	1.25	168	T	0	24
IRW	IWB59469	6B	87.52	2.37	4.175	85.27	89.77	C	-1.21	169	T	0	23
IRW	IWB73456	6B	90.33	3.34	6.338	88.08	92.58	C	2.94	21	T	0	171
IRW	IWA3947	6B	152.28	2.21	3.83	150.03	154.53	A	-0.96	44	G	0	148
IRW	IWB45867	7A	91.82	2.89	5.331	89.57	94.07	G	1.55	164	T	0	28
IRW	IWB11841	7A	94.72	3.16	5.944	92.47	96.97	C	-1.43	66	T	0	126
IRW	IWB32122	7A	107.7	2.12	3.639	105.45	109.95	C	4.21	169	T	0	23
IRW	IWB73705	7A	150.94	2.20	3.801	148.69	153.19	C	-2.44	18	T	0	174
IRW	IWB71711	7A	204.2	2.35	4.129	201.95	206.45	C	2.63	13	T	0	179
IRW	IWB72335	7B	58.34	2.75	5.001	56.09	60.59	A	-1.58	16	C	0	176
IRW	IWB30711	7B	72.81	2.14	3.683	70.56	75.06	A	-1.07	125	G	0	67
IRW	IWB35797	7B	112.52	2.94	5.435	110.27	114.77	A	-2.77	169	G	0	23
iTGW	IWB2101	1A	94.71	2.17	3.953	92.46	96.96	A	-2.75	71	C	0	121
iTGW	IWB62270	1B	115.78	2.10	3.805	113.53	118.03	C	2.31	145	T	0	47
iTGW	IWB3081	1B	136.61	2.34	4.342	134.36	138.86	C	2.97	66	T	0	126
iTGW	IWA6768	2B	24.62	2.09	3.779	22.37	26.87	A	-4.88	144	G	0	48
iTGW	IWB11852	3A	5.33	2.15	3.897	3.08	7.58	A	-5.68	177	C	0	15
iTGW	IWB50218	3A	119.56	2.05	3.678	117.31	121.81	C	5.87	30	T	0	162
iTGW	IWB69546	3A	165.91	2.28	4.208	163.66	168.16	C	3.83	36	T	0	156
iTGW	IWB21932	3B	2.45	2.57	4.874	0.2	4.7	A	2.65	100	G	0	92

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
iTGW	IWA3046	3B	123	2.45	4.594	120.75	125.25	A	-5.19	178	G	0	14
iTGW	IWB65507	3B	126.23	4.15	8.706	123.98	128.48	A	-9.84	160	G	0	32
iTGW	IWB11298	3B	129.61	3.87	8.007	127.36	131.86	A	10.94	160	C	0	32
iTGW	IWB45539	3B	200.53	2.02	3.612	198.28	202.78	C	3.69	179	T	0	13
iTGW	IWB50550	4A	140.69	2.16	3.923	138.44	142.94	A	-4.25	37	G	0	155
iTGW	IWB45635	5B	12.43	2.56	4.851	10.18	14.68	C	-4.48	148	T	0	44
iTGW	IWA7223	5B	15.89	2.04	3.654	13.64	18.14	A	-4.46	12	G	0	180
iTGW	IWA279	5B	40.43	2.10	3.8	38.18	42.68	C	3.48	131	T	0	61
iTGW	IWA8569	5B	43.4	2.22	4.071	41.15	45.65	A	5.03	65	G	0	127
iTGW	IWB25222	5B	59.61	2.11	3.827	57.36	61.86	C	-3.43	88	T	0	104
iTGW	IWB71812	5B	140.55	2.19	4.002	138.3	142.8	A	-3.19	142	G	0	50
iTGW	IWB34573	6A	4.81	2.17	3.962	2.56	7.06	A	-3.12	79	G	0	113
iTGW	IWB63300	6A	126.51	2.35	4.362	124.26	128.76	A	-3.22	66	G	0	126
iTGW	IWB51312	6B	85.4	2.66	5.075	83.15	87.65	A	5.94	182	G	0	10
iTGW	IWB43059	6B	105.51	2.13	3.866	103.26	107.76	C	3.60	27	T	0	165
iTGW	IWB10034	6B	121.71	2.13	3.866	119.46	123.96	C	3.35	27	T	0	165
iTGW	IWB58575	7A	0.92	2.46	4.627	0	3.17	C	3.99	42	T	0	150
iTGW	IWA6475	7A	49.8	2.87	5.574	47.55	52.05	C	5.05	38	T	0	154
iTGW	IWB27639	7A	53.11	2.24	4.123	50.86	55.36	A	3.92	42	C	0	150
iTGW	IWB7752	7A	98.3	3.35	6.73	96.05	100.55	A	-7.27	173	G	0	19
iTGW	IWB10556	7A	140.01	2.52	4.77	137.76	142.26	C	-3.00	113	T	0	79
iTGW	IWB69294	7A	148.02	2.14	3.876	145.77	150.27	A	-5.15	182	C	0	10
iTGW	IWB60	7B	33.71	3.31	6.644	31.46	35.96	A	3.83	28	C	0	164
iTGW	IWB58837	7B	210.01	2.07	3.718	207.76	212.26	C	2.82	150	T	0	42
RDW	IWB68479	1A	106.2	2.52	4.421	103.95	108.45	C	7.86	87	T	0	105
RDW	IWB29244	1A	123.21	2.26	3.855	120.96	125.46	C	-6.29	138	T	0	54

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
RDW	IWB31719	1A	139.9	2.04	3.406	137.65	142.15	G	13.17	18	T	0	174
RDW	IWB60732	1B	33.75	3.55	6.717	31.5	36	A	10.59	41	G	0	151
RDW	IWB62079	1B	162.54	2.10	3.519	160.29	164.79	A	-9.10	36	G	0	156
RDW	IWB53380	2A	35.63	2.38	4.118	33.38	37.88	A	15.61	159	G	0	33
RDW	IWB26349	2A	156.31	2.11	3.549	154.06	158.56	G	18.64	19	T	0	173
RDW	IWB5627	2B	140.42	2.77	4.975	138.17	142.67	A	6.11	105	G	0	87
RDW	IWB30420	2B	174.3	2.07	3.472	172.05	176.55	A	-12.68	34	G	0	158
RDW	IWB7580	2B	182.72	2.11	3.551	180.47	184.97	A	-36.37	166	G	0	26
RDW	IWB67049	3A	80.8	3.17	5.761	78.55	83.05	A	-14.10	15	G	0	177
RDW	IWA6914	3A	83.73	2.04	3.409	81.48	85.98	C	5.61	59	T	0	133
RDW	IWB35437	3B	41.34	2.55	4.489	39.09	43.59	C	-13.65	36	T	0	156
RDW	IWB21309	4A	17.01	4.34	8.409	14.76	19.26	C	-9.18	87	T	0	105
RDW	IWA1219	4A	64.9	2.24	3.828	62.65	67.15	A	7.49	106	G	0	86
RDW	IWB35047	4B	80.4	2.07	3.463	78.15	82.65	C	-7.43	91	G	0	101
RDW	IWB23476	4B	114.43	2.19	3.704	112.18	116.68	A	14.19	154	C	0	38
RDW	IWA3196	5A	16.83	2.05	3.422	14.58	19.08	C	40.29	26	T	0	166
RDW	IWB64985	5B	179.43	2.31	3.975	177.18	181.68	C	6.21	128	T	0	64
RDW	IWB47364	5B	181.92	2.52	4.411	179.67	184.17	A	10.29	178	G	0	14
RDW	IWB75083	6B	43.2	2.01	3.336	40.95	45.45	A	5.91	33	G	0	159
RDW	IWB8142	7A	87.71	2.50	4.377	85.46	89.96	A	-7.74	77	G	0	115
RDW	IWB7926	7A	91.22	2.01	3.332	88.97	93.47	A	6.55	137	G	0	55
RDW	IWB11841	7A	94.72	2.39	4.142	92.47	96.97	C	-7.63	66	T	0	126
RDW	IWB24060	7B	25.43	2.06	3.447	23.18	27.68	A	5.30	149	G	0	43
RDW	IWB30711	7B	72.81	2.17	3.671	70.56	75.06	A	-6.04	125	G	0	67
RDW	IWB42040	7B	75.79	2.42	4.211	73.54	78.04	C	8.09	160	A	0	32
RGA	IWA6253	1A	120.07	2.73	5.359	117.82	122.32	A	13.52	157	G	0	35

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
RGA	IWB47315	2B	89.9	2.44	4.663	87.65	92.15	G	16.39	172	T	0	20
RGA	IWB68278	2B	110.2	2.11	3.896	107.95	112.45	C	13.84	75	T	0	117
RGA	IWB30560	2B	140.32	2.03	3.698	138.07	142.57	G	13.59	30	T	0	162
RGA	IWB5933	3A	170.11	2.10	3.868	167.86	172.36	C	-4.81	89	T	0	103
RGA	IWB13827	3B	10.41	2.18	4.047	8.16	12.66	A	10.34	119	G	0	73
RGA	IWB37373	3B	64.63	2.07	3.795	62.38	66.88	A	-14.50	15	G	0	177
RGA	IWB43503	4A	41.33	2.65	5.167	39.08	43.58	C	-14.15	154	T	0	38
RGA	IWB32978	4A	44.61	2.28	4.292	42.36	46.86	A	14.32	29	C	0	163
RGA	IWB57437	4A	49.54	2.40	4.575	47.29	51.79	A	12.47	85	G	0	107
RGA	IWB69385	4A	167.15	3.15	6.378	164.9	169.4	G	13.44	78	T	0	114
RGA	IWB11140	5B	11.4	2.32	4.369	9.15	13.65	A	13.92	63	C	0	129
RGA	IWB11919	5B	167.62	2.18	4.055	165.37	169.87	C	21.13	34	T	0	158
RGA	IWB4410	5B	193.81	2.55	4.912	191.56	196.06	A	-12.36	110	G	0	82
RGA	IWB64082	6A	0.18	2.81	5.536	-2.07	2.43	C	-15.40	168	T	0	24
RGA	IWB13180	6A	75.21	2.23	4.169	72.96	77.46	C	12.23	64	T	0	128
RGA	IWB70344	6A	105.73	2.75	5.392	103.48	107.98	A	13.68	118	G	0	74
RGA	IWB49974	6A	110.3	2.71	5.304	108.05	112.55	A	-16.29	106	G	0	86
RGA	IWA4603	6A	117.72	2.81	5.548	115.47	119.97	A	-15.72	96	G	0	96
RGA	IWB37899	6A	119	2.78	5.472	116.75	121.25	C	-11.05	147	T	0	45
RGA	IWB71119	6A	122.43	6.85	16.08	120.18	124.68	C	-22.31	113	T	0	79
RGA	IWB45975	6B	112.94	2.04	3.738	110.69	115.19	A	12.55	165	G	0	27
RGA	IWB11249	7A	9.82	2.15	3.979	7.57	12.07	C	-13.63	26	T	0	166
RGA	IWB9770	7A	150.92	2.18	4.047	148.67	153.17	C	-12.43	55	T	0	137
RGA	IWB26105	7B	15.23	2.09	3.85	12.98	17.48	C	-9.56	120	T	0	72
RGA	IWB48843	7B	138.57	2.52	4.859	136.32	140.82	C	15.94	42	T	0	150
RSR	IWB8796	1A	10.62	2.88	4.357	8.37	12.87	A	0.07	11	G	0	181

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
RSR	IWA1481	1A	16.55	2.19	3.101	14.3	18.8	C	-0.07	21	T	0	171
RSR	IWB31742	1B	135.34	2.04	2.84	133.09	137.59	A	-0.07	179	G	0	13
RSR	IWB72561	1B	140.1	2.34	3.369	137.85	142.35	C	0.07	14	T	0	178
RSR	IWA724	1B	152.61	2.70	4.021	150.36	154.86	A	0.04	114	G	0	78
RSR	IWB60432	1B	155.45	2.46	3.579	153.2	157.7	A	0.05	167	G	0	25
RSR	IWB26349	2A	156.31	2.54	3.732	154.06	158.56	G	0.09	19	T	0	173
RSR	IWA7936	2B	19.03	2.32	3.338	16.78	21.28	A	0.13	167	G	0	25
RSR	IWB11285	2B	71.01	2.14	3.021	68.76	73.26	A	0.04	95	G	0	97
RSR	IWA4102	2B	84.05	2.08	2.916	81.8	86.3	A	0.04	29	G	0	163
RSR	IWB7580	2B	182.72	2.15	3.032	180.47	184.97	A	-0.16	166	G	0	26
RSR	IWB25948	3A	96.93	3.02	4.618	94.68	99.18	C	-0.10	170	T	0	22
RSR	IWB11298	3B	129.61	2.07	2.887	127.36	131.86	A	-0.08	160	C	0	32
RSR	IWB11701	3B	205.82	2.29	3.279	203.57	208.07	A	0.10	169	C	0	23
RSR	IWA4445	5A	0.72	2.38	3.436	-1.53	2.97	A	-0.07	179	G	0	13
RSR	IWA5612	5A	100.64	2.05	2.864	98.39	102.89	A	0.05	165	G	0	27
RSR	IWA1394	5B	38.12	2.55	3.753	35.87	40.37	A	0.04	116	G	0	76
RSR	IWB33626	6A	41.07	2.05	2.857	38.82	43.32	C	-0.07	18	T	0	174
RSR	IWB53682	6B	103.81	2.14	3.016	101.56	106.06	A	-0.05	176	G	0	16
RSR	IWB73688	7A	61.64	2.80	4.196	59.39	63.89	C	-0.04	96	T	0	96
RSR	IWB71114	7B	8.51	2.07	2.886	6.26	10.76	C	-0.07	13	T	0	179
RSR	IWB73292	7B	44.32	2.46	3.592	42.07	46.57	A	-0.08	175	G	0	17
RSR	IWB747	7B	211.71	2.28	3.265	209.46	213.96	G	0.08	17	T	0	175
RT6	IWB27591	1A	20.72	2.17	3.746	18.47	22.97	A	-0.21	149	C	0	43
RT6	IWB53186	1A	65.09	2.08	3.556	62.84	67.34	A	-0.22	69	G	0	123
RT6	IWB11628	1A	76.91	2.32	4.077	74.66	79.16	A	-0.27	75	G	0	117
RT6	IWB31719	1A	139.9	2.17	3.751	137.65	142.15	G	0.29	18	T	0	174

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
RT6	IWA1560	1A	142.73	2.66	4.815	140.48	144.98	C	0.22	133	T	0	59
RT6	IWB35568	1B	27.21	2.18	3.757	24.96	29.46	A	0.22	111	G	0	81
RT6	IWB55711	2B	53.04	2.07	3.521	50.79	55.29	A	0.14	122	G	0	70
RT6	IWB70307	2B	128.76	2.56	4.6	126.51	131.01	G	-0.17	63	T	0	129
RT6	IWB5627	2B	140.42	2.45	4.364	138.17	142.67	A	0.13	105	G	0	87
RT6	IWA1324	2B	165.93	2.07	3.526	163.68	168.18	G	-0.24	46	T	0	146
RT6	IWB12651	3A	148.51	2.27	3.952	146.26	150.76	C	-0.26	38	T	0	154
RT6	IWB11860	3B	100.54	2.14	3.684	98.29	102.79	C	0.26	19	T	0	173
RT6	IWB50513	3B	148.42	2.82	5.175	146.17	150.67	G	0.20	144	T	0	48
RT6	IWB21309	4A	17.01	2.70	4.902	14.76	19.26	C	-0.18	87	T	0	105
RT6	IWA1137	4A	25.8	2.26	3.946	23.55	28.05	A	-0.43	168	G	0	24
RT6	IWB72884	4B	45.01	3.68	7.131	42.76	47.26	A	0.21	138	G	0	54
RT6	IWB35047	4B	80.4	3.45	6.618	78.15	82.65	C	-0.22	91	G	0	101
RT6	IWB66095	4B	91.74	3.32	6.303	89.49	93.99	C	0.28	47	T	0	145
RT6	IWB74035	5B	175.69	2.30	4.029	173.44	177.94	C	0.18	95	T	0	97
RT6	IWB55144	5B	189.77	2.17	3.739	187.52	192.02	C	0.19	112	T	0	80
RT6	IWB4117	6A	30.5	2.01	3.405	28.25	32.75	A	-0.08	59	G	0	133
RT6	IWB75083	6B	43.2	2.03	3.445	40.95	45.45	A	0.16	33	G	0	159
RT6	IWB60487	6B	71.52	2.61	4.704	69.27	73.77	C	-0.23	153	T	0	39
RT6	IWB10268	6B	139.19	2.03	3.447	136.94	141.44	C	-0.19	147	T	0	45
RT6	IWB27639	7A	53.11	2.36	4.161	50.86	55.36	A	-0.18	43	C	0	149
RT6	IWB56095	7A	147.42	2.29	4.008	145.17	149.67	C	0.18	166	T	0	26
RT6	IWB5306	7B	177.23	2.28	3.978	174.98	179.48	A	0.14	119	G	0	73
SDW	IWB68479	1A	106.2	2.05	3.554	103.95	108.45	C	7.63	87	T	0	105
SDW	IWB29244	1A	123.21	3.33	6.267	120.96	125.46	C	-9.18	138	T	0	54
SDW	IWB31719	1A	139.9	2.07	3.606	137.65	142.15	G	13.43	18	T	0	174

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
SDW	IWB60732	1B	33.75	3.38	6.581	31.5	36	A	13.40	41	G	0	151
SDW	IWB48378	1B	162.11	2.11	3.694	159.86	164.36	C	-11.47	36	T	0	156
SDW	IWB53380	2A	35.63	2.64	4.877	33.38	37.88	A	20.79	159	G	0	33
SDW	IWB5627	2B	140.42	2.13	3.73	138.17	142.67	A	5.64	105	G	0	87
SDW	IWB67049	3A	80.8	2.57	4.763	78.55	83.05	A	-12.64	15	G	0	177
SDW	IWB35437	3B	41.34	3.10	5.93	39.09	43.59	C	-17.51	36	T	0	156
SDW	IWB36039	3B	64.62	2.44	4.42	62.37	66.87	T	-7.81	135	C	0	57
SDW	IWB21309	4A	17.01	3.82	7.392	14.76	19.26	C	-8.20	87	T	0	105
SDW	IWA1219	4A	64.9	2.97	5.631	62.65	67.15	A	10.41	106	G	0	86
SDW	IWB12737	4A	110.92	2.12	3.709	108.67	113.17	A	-13.98	158	G	0	34
SDW	IWB35047	4B	80.4	2.25	4.011	78.15	82.65	C	-8.26	91	G	0	101
SDW	IWB23476	4B	114.43	3.23	6.026	112.18	116.68	A	15.41	154	C	0	38
SDW	IWB11967	5A	85.61	2.64	4.869	83.36	87.86	A	-11.42	176	G	0	16
SDW	IWB47364	5B	181.92	2.33	4.189	179.67	184.17	A	12.56	175	G	0	17
SDW	IWB8808	5B	190.51	3.09	5.725	188.26	192.76	A	-9.41	36	C	0	156
SDW	IWB21773	6B	85.92	2.03	3.515	83.67	88.17	A	9.48	173	G	0	19
SDW	IWB8142	7A	87.71	2.63	4.847	85.46	89.96	A	-9.48	77	G	0	115
SDW	IWA7419	7A	90.73	2.04	3.532	88.48	92.98	G	-7.61	81	T	0	111
TRL	IWB9746	1A	109.9	2.72	5.038	107.65	112.15	A	-9.01	62	C	0	130
TRL	IWB47703	1A	122.75	2.93	5.528	120.5	125	C	-5.37	54	T	0	138
TRL	IWB8771	1A	148	2.65	4.881	145.75	150.25	A	-0.01	178	G	0	14
TRL	IWB11309	1B	30.52	2.72	5.037	28.27	32.77	C	7.29	120	T	0	72
TRL	IWB60732	1B	33.75	3.46	6.746	31.5	36	A	16.08	41	G	0	151
TRL	IWB56695	1B	77.32	2.17	3.813	75.07	79.57	C	-7.79	68	T	0	124
TRL	IWB66543	1B	141.31	2.34	4.197	139.06	143.56	C	5.30	120	T	0	72
TRL	IWB53380	2A	35.63	2.77	5.166	33.38	37.88	A	20.30	159	G	0	33

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
TRL	IWB5627	2B	140.42	2.05	3.556	138.17	142.67	A	9.04	105	G	0	87
TRL	IWB29332	2B	160.51	2.12	3.701	158.26	162.76	A	5.50	24	G	0	168
TRL	IWB7306	3A	141.51	2.15	3.765	139.26	143.76	A	-15.01	171	G	0	21
TRL	IWB57554	3B	2.83	2.02	3.496	0.58	5.08	A	14.81	182	G	0	10
TRL	IWB35437	3B	41.34	2.91	5.476	39.09	43.59	C	-14.64	36	T	0	156
TRL	IWB49982	3B	46.22	2.15	3.777	43.97	48.47	A	7.12	155	G	0	37
TRL	IWB8954	3B	49.7	2.15	3.777	47.45	51.95	A	7.12	155	G	0	37
TRL	IWB36039	3B	64.62	2.73	5.053	62.37	66.87	C	-6.06	135	T	0	57
TRL	IWA1219	4A	64.9	2.15	3.765	62.65	67.15	A	2.66	106	G	0	86
TRL	IWB12737	4A	110.92	2.02	3.485	108.67	113.17	A	-6.40	158	G	0	34
TRL	IWB23476	4B	114.43	3.12	5.667	112.18	116.68	A	8.80	154	C	0	38
TRL	IWA3196	5A	16.83	3.07	5.567	14.58	19.08	C	39.84	126	T	0	66
TRL	IWB11967	5A	85.61	2.17	3.813	83.36	87.86	A	-18.08	176	G	0	16
TRL	IWB47364	5B	181.92	2.78	5.184	179.67	184.17	A	13.47	175	G	0	17
TRL	IWB73456	6B	90.33	2.16	3.783	88.08	92.58	C	-0.72	21	T	0	171
TRL	IWB62163	6B	145.91	2.07	3.596	143.66	148.16	A	-0.77	65	C	0	127
TRL	IWB2097	6B	152.21	2.46	4.45	149.96	154.46	A	-1.09	58	G	0	134
TRL	IWB6290	7A	11.1	2.27	4.03	8.85	13.35	C	-0.20	76	T	0	116
TRL	IWB47901	7A	14.22	2.15	3.766	11.97	16.47	A	0.20	115	G	0	77
TRL	IWB11906	7A	91.23	2.44	4.412	88.98	93.48	C	-8.57	55	T	0	137
TRL	IWB11841	7A	94.72	2.89	5.432	92.47	96.97	C	-8.93	66	T	0	126
TRL	IWB30711	7B	72.81	2.58	4.721	70.56	75.06	A	-4.57	125	G	0	67
TRN	IWB8696	1A	5.2	3.07	5.711	2.95	7.45	A	0.78	31	G	0	161
TRN	IWB12589	1A	13.62	3.34	6.317	11.37	15.87	A	0.57	16	G	0	176
TRN	IWB35568	1B	27.21	3.39	6.432	24.96	29.46	A	0.54	111	G	0	81
TRN	IWB22675	2B	87.31	2.01	3.383	85.06	89.56	A	-0.45	20	G	0	172

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
TRN	IWB70307	2B	128.76	2.03	3.427	126.51	131.01	G	-0.32	63	T	0	129
TRN	IWB35157	3A	71.81	2.28	3.956	69.56	74.06	G	-0.31	92	T	0	100
TRN	IWB36021	3B	4.5	2.22	3.837	2.25	6.75	C	0.32	44	T	0	148
TRN	IWB50786	3B	19.4	2.14	3.657	17.15	21.65	A	0.45	21	G	0	171
TRN	IWA5324	3B	138.42	2.12	3.616	136.17	140.67	C	0.38	62	T	0	130
TRN	IWB50513	3B	148.42	2.87	5.253	146.17	150.67	G	0.41	144	T	0	48
TRN	IWB21309	4A	17.01	3.69	7.132	14.76	19.26	C	-0.43	87	T	0	105
TRN	IWB10265	4B	44.92	3.14	5.869	42.67	47.17	A	0.39	138	G	0	54
TRN	IWB35047	4B	80.4	3.59	6.901	78.15	82.65	C	-0.44	91	G	0	101
TRN	IWB66095	4B	91.74	3.37	6.388	89.49	93.99	C	0.52	47	T	0	145
TRN	IWA5086	5B	40.78	2.15	3.686	38.53	43.03	C	0.40	30	T	0	162
TRN	IWB64602	5B	189.77	2.43	4.29	187.52	192.02	A	0.38	112	G	0	80
TRN	IWB45770	6A	60.02	2.41	4.24	57.77	62.27	A	-0.38	62	G	0	130
TRN	IWB28178	6B	69.95	2.17	3.732	67.7	72.2	C	-0.41	75	T	0	117
TRN	IWB6290	7A	11.1	2.10	3.568	8.85	13.35	C	0.31	76	T	0	116
TRN	IWB3767	7A	146.9	3.07	5.719	144.65	149.15	C	0.50	171	T	0	21
TRN	IWA6901	7B	28.54	2.03	3.435	26.29	30.79	A	0.39	59	G	0	133

Appendix Table 5. Allelic distribution and their effect on root growth angle (RGA) of QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by RGA.

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP011	45.76		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP014	47.82		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP077	51.26		TT	TT	GG	CC	TT	AA	GG	GG	CC
EP019	51.63		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP042	57.61		CC	TT	AA	CC	CC	AA	GG	AA	CC
EP074	57.87		CC	TT	AA	TT	CC	GG	GG	AA	CC
EP036	59.11		CC	GG	AA	CC	CC	GG	GG	AA	TT
EP010	60.40		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP087	61.39		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP044	62.59		TT	TT	GG	TT	CC	AA	AA	GG	CC
EP034	63.93		CC	TT	AA	CC	CC	AA	GG	AA	CC
EP070	66.64		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP068	66.84		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP095	68.00		CC	TT	AA	CC	CC	AA	AA	GG	CC
EP069	68.99		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP127	71.17		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP041	71.95		CC	TT	AA	CC	CC	AA	GG	AA	CC
EP110	72.20		TT	GG	AA	CC	CC	GG	GG	AA	CC
EP015	75.92		CC	GG	AA	CC	CC	GG	AA	AA	TT
EP128	76.01		TT	TT	GG	CC	CC	AA	AA	GG	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP166	76.33		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP088	76.38		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP003	76.40		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP020	76.64		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP188	77.74		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP097	78.20		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP170	78.47		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP108	79.11		CC	GG	AA	CC	CC	GG	GG	AA	CC
EP109	80.53		CC	TT	AA	CC	CC	AA	GG	AA	CC
EP137	80.54		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP080	81.57		CC	TT	AA	CC	CC	GG	AA	AA	TT
EP021	81.58		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP154	82.74		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP079	83.25		CC	TT	AA	CC	CC	GG	AA	AA	TT
EP049	83.46		CC	TT	AA	TT	CC	GG	GG	AA	TT
EP038	83.50		CC	TT	AA	CC	CC	AA	AA	AA	CC
EP118	83.57		TT	TT	AA	CC	TT	AA	AA	AA	CC
EP030	83.60		CC	TT	GG	CC	CC	AA	AA	GG	CC
EP096	83.68		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP136	84.10		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP126	84.47		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP062	85.22		TT	TT	GG	CC	CC	AA	AA	GG	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP133	85.51		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP094	85.67		CC	TT	AA	CC	CC	AA	AA	AA	CC
EP150	86.30		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP084	86.45		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP064	86.50		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP130	86.77		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP039	87.01		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP075	87.60		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP186	87.84		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP022	87.87		CC	TT	AA	CC	CC	AA	AA	AA	CC
EP185	88.06		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP107	88.19		CC	TT	GG	CC	CC	AA	GG	AA	CC
EP002	89.54		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP004	89.87		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP072	90.75		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP057	90.84		CC	GG	AA	CC	CC	GG	AA	AA	TT
EP180	90.90		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP076	90.95		CC	TT	AA	CC	CC	GG	GG	AA	CC
EP129	91.23		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP175	91.50		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP089	92.05		TT	GG	GG	TT	TT	AA	AA	GG	TT
EP176	92.24		CC	GG	AA	CC	CC	GG	AA	AA	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP194	92.33		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP197	92.34		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP113	92.84		CC	GG	AA	CC	CC	AA	AA	AA	CC
EP117	92.97		TT	GG	AA	CC	CC	AA	AA	AA	CC
EP182	93.47		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP183	93.64		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP017	93.67		CC	GG	AA	CC	CC	GG	AA	AA	TT
EP085	93.71		CC	GG	AA	CC	CC	GG	AA	AA	TT
EP187	93.74		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP132	94.26		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP184	94.34		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP156	94.40		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP112	94.42		TT	GG	AA	CC	TT	AA	AA	AA	CC
EP167	94.44		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP083	94.57		CC	TT	AA	TT	CC	GG	GG	AA	CC
EP173	95.24		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP008	95.41		TT	GG	GG	CC	CC	AA	AA	GG	CC
EP086	95.45		CC	GG	AA	TT	CC	GG	AA	AA	CC
EP045	95.68		CC	GG	AA	CC	CC	AA	AA	AA	TT
EP131	95.77		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP026	96.40		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP193	96.44		CC	GG	AA	CC	CC	GG	AA	AA	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP098	97.11		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP192	97.50		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP134	97.63		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP111	97.73		CC	TT	AA	CC	CC	GG	GG	AA	CC
EP146	98.04		TT	TT	GG	CC	CC	AA	AA	GG	TT
EP195	98.17		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP169	98.27		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP043	98.83		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP155	99.30		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP122	99.56		CC	TT	AA	CC	CC	AA	AA	AA	CC
EP120	99.60		TT	TT	GG	CC	TT	AA	AA	AA	CC
EP135	100.03		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP082	101.08		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP158	101.37		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP051	101.62		TT	GG	GG	TT	TT	AA	AA	GG	CC
EP179	101.77		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP124	101.91		CC	TT	GG	CC	TT	AA	AA	AA	CC
EP091	102.00		TT	GG	GG	TT	TT	AA	AA	GG	TT
EP190	102.14		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP037	102.18		CC	TT	AA	CC	CC	AA	GG	AA	CC
EP164	102.51		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP024	102.56		TT	TT	GG	CC	TT	AA	AA	GG	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP172	102.58		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP160	102.64		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP159	102.90		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP028	103.08		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP048	103.14		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP023	103.29		TT	TT	GG	CC	TT	AA	GG	GG	TT
EP141	103.30		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP119	103.76		TT	GG	GG	CC	TT	AA	GG	AA	CC
EP105	104.00		CC	GG	AA	CC	CC	AA	GG	AA	CC
EP174	104.07		TT	GG	AA	CC	TT	AA	AA	AA	CC
EP047	104.80		TT	TT	GG	CC	CC	AA	AA	AA	TT
EP142	104.83		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP196	105.14		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP078	105.14		TT	TT	GG	TT	TT	AA	AA	GG	CC
EP145	105.30		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP163	105.58		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP162	106.13		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP189	106.17		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP152	106.20		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP191	106.27		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP016	106.39		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP139	106.43		TT	TT	GG	CC	CC	AA	AA	GG	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP025	106.93		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP071	107.55		CC	TT	AA	CC	CC	GG	AA	AA	CC
EP106	107.80		TT	GG	AA	CC	TT	AA	AA	AA	CC
EP115	107.96		TT	GG	AA	CC	TT	GG	AA	AA	CC
EP165	108.01		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP093	108.27		TT	GG	GG	TT	TT	AA	AA	GG	TT
EP006	108.42		TT	GG	AA	TT	CC	AA	AA	GG	TT
EP147	108.59		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP116	108.84		TT	GG	GG	CC	TT	AA	GG	AA	CC
EP092	108.89		TT	GG	GG	TT	TT	AA	AA	GG	TT
EP200	108.90		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP143	109.08		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP059	109.15		TT	GG	AA	TT	TT	GG	GG	AA	TT
EP140	109.36		TT	TT	GG	CC	CC	AA	AA	GG	TT
EP065	109.73		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP199	109.80		TT	GG	GG	CC	CC	AA	AA	GG	CC
EP144	109.94		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP157	110.01		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP138	110.37		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP033	110.47		CC	GG	AA	CC	CC	GG	GG	AA	TT
EP168	110.68		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP060	110.89		TT	GG	GG	TT	TT	AA	AA	GG	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP099	111.23		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP149	111.23		TT	TT	GG	CC	CC	AA	GG	GG	CC
EP058	111.55		TT	GG	GG	TT	CC	AA	AA	AA	CC
EP181	111.87		CC	GG	AA	CC	CC	GG	AA	AA	CC
EP153	112.29		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP029	112.93		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP046	113.12		TT	TT	GG	TT	CC	AA	AA	AA	TT
EP103	113.24		TT	GG	AA	CC	CC	GG	AA	AA	CC
EP032	113.87		TT	GG	AA	CC	TT	GG	GG	AA	TT
EP067	114.54		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP005	115.04		CC	GG	AA	CC	CC	AA	AA	AA	TT
EP171	115.07		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP013	115.10		CC	GG	AA	CC	CC	GG	AA	AA	TT
EP101	115.31		TT	GG	AA	CC	TT	AA	AA	AA	CC
EP050	115.84		TT	GG	GG	TT	TT	AA	AA	GG	CC
EP050	115.84		TT	GG	GG	TT	TT	AA	AA	GG	CC
EP063	115.90		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP100	116.14		TT	TT	GG	CC	TT	AA	AA	GG	CC
EP114	116.34		TT	GG	GG	CC	TT	AA	GG	AA	CC
EP198	116.37		TT	GG	GG	CC	CC	AA	AA	GG	CC
EP121	117.17		TT	GG	GG	CC	TT	AA	GG	AA	CC
EP123	117.74		TT	GG	GG	CC	CC	AA	AA	AA	CC

Accession	RGA	QTL-tagging markers	IWB71119	IWB69385	IWA4603	IWB64082	IWB37899	IWB70344	IWA6253	IWB49974	IWB43503
		alleles	C/T	G/T	A/G	C/T	C/T	A/G	A/G	A/G	C/T
		chrom	6A	4A	6A	6A	6A	6A	1A	6A	4A
		cM	122.43	167.15	117.72	0.18	119	105.73	120.07	110.3	41.33
		-LOG10 P	6.85	3.15	2.81	2.81	2.78	2.75	2.73	2.71	2.65
		R ² (%)	16.08	6.38	5.55	5.54	5.47	5.39	5.36	5.30	5.17
		Allelic Effect	-22.31	13.44	-15.72	-15.4	-11.05	13.68	13.52	16.29	14.15
EP090	118.20		TT	GG	GG	TT	TT	AA	AA	GG	TT
EP018	119.08		TT	TT	GG	CC	TT	AA	AA	GG	TT
EP125	119.40		TT	GG	AA	CC	TT	AA	AA	AA	CC
EP031	119.43		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP001	120.28		TT	GG	GG	CC	TT	AA	AA	GG	CC
EP054	120.37		TT	GG	AA	TT	TT	GG	AA	AA	TT
EP009	120.66		TT	GG	AA	CC	TT	GG	AA	AA	TT
EP055	121.00		TT	GG	AA	TT	CC	GG	AA	AA	TT
EP066	121.33		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP012	121.52		CC	GG	AA	TT	CC	GG	AA	AA	TT
EP081	121.97		CC	TT	AA	CC	CC	GG	AA	AA	TT
EP052	122.43		TT	GG	AA	TT	TT	GG	AA	AA	TT
EP007	122.60		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP104	123.35		TT	GG	AA	CC	CC	AA	AA	AA	CC
EP053	123.52		TT	GG	AA	TT	TT	GG	AA	AA	TT
EP151	123.76		TT	TT	GG	CC	CC	AA	AA	GG	CC
EP102	124.17		TT	TT	GG	CC	TT	AA	AA	GG	TT
SNP allele frequency			CC	TT	AA	CC	CC	GG	GG	AA	CC
			0.42	0.6	0.51	0.88	0.78	0.39	0.18	0.55	0.81
SNP allele frequency			TT	GG	GG	TT	TT	AA	AA	GG	TT
			0.58	0.4	0.49	0.12	0.22	0.61	0.82	0.55	0.19
SNP allele contributin for narrow RGA				SNP allele contributin for wide RGA							

Appendix Table 6. Allelic distribution for total root number (TRN) QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by TRN.

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP059	3.47		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP087	3.53		CC	GG	AA	TT	GG	GG	TT	GG	GG
EP089	3.54		CC	CC	AA	TT	GG	GG	TT	GG	GG
EP028	3.66		TT	CC	GG	TT	GG	GG	TT	GG	TT
EP105	3.73		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP066	3.91		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP045	3.94		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP069	3.99		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP026	4.10		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP062	4.27		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP136	4.32		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP135	4.33		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP007	4.42		CC	CC	GG	TT	GG	AA	CC	GG	TT
EP064	4.51		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP063	4.55		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP146	4.55		TT	CC	GG	TT	GG	GG	CC	GG	TT
EP052	4.55		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP070	4.56		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP048	4.56		CC	CC	GG	TT	AA	AA	CC	GG	GG
EP042	4.59		TT	CC	AA	TT	AA	AA	CC	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP076	4.59		CC	CC	AA	TT	GG	AA	CC	GG	GG
EP023	4.65		CC	CC	GG	TT	GG	GG	TT	GG	GG
EP058	4.65		TT	GG	GG	TT	GG	GG	CC	GG	TT
EP060	4.66		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP141	4.68		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP001	4.68		CC	CC	GG	TT	GG	GG	CC	GG	GG
EP199	4.69		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP102	4.69		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP145	4.70		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP010	4.72		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP012	4.77		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP113	4.77		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP054	4.78		TT	GG	GG	TT	GG	AA	CC	GG	GG
EP147	4.78		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP091	4.78		CC	CC	AA	TT	GG	GG	TT	GG	GG
EP084	4.79		TT	GG	AA	TT	GG	AA	CC	GG	TT
EP065	4.80		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP166	4.80		TT	CC	GG	TT	GG	GG	TT	GG	GG
EP002	4.80		CC	CC	GG	TT	GG	GG	TT	GG	GG
EP119	4.81		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP183	4.83		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP144	4.85		TT	CC	GG	TT	GG	GG	CC	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP106	4.85		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP006	4.86		TT	CC	AA	TT	GG	AA	CC	GG	TT
EP067	4.86		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP025	4.88		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP037	4.89		TT	CC	AA	TT	AA	AA	CC	GG	GG
EP103	4.91		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP019	4.91		CC	GG	AA	TT	GG	AA	CC	GG	GG
EP188	4.91		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP112	4.91		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP093	4.92		CC	CC	AA	TT	GG	GG	TT	GG	GG
EP011	4.93		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP074	4.95		TT	GG	AA	TT	GG	AA	CC	GG	TT
EP056	4.96		TT	GG	AA	CC	GG	AA	CC	GG	GG
EP055	4.96		TT	CC	AA	TT	GG	AA	CC	GG	GG
EP175	4.96		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP072	4.97		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP043	4.98		TT	GG	AA	TT	GG	AA	TT	GG	GG
EP096	4.99		CC	CC	AA	TT	GG	AA	CC	GG	GG
EP068	5.00		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP124	5.01		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP121	5.01		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP137	5.02		TT	CC	GG	TT	GG	AA	CC	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP015	5.03		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP140	5.03		TT	CC	GG	TT	GG	GG	CC	GG	TT
EP190	5.03		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP005	5.06		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP100	5.06		TT	CC	AA	TT	GG	GG	TT	GG	GG
EP138	5.08		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP198	5.08		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP122	5.09		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP196	5.09		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP110	5.10		CC	GG	AA	CC	GG	GG	TT	AA	GG
EP107	5.11		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP104	5.11		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP174	5.12		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP194	5.12		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP008	5.13		TT	CC	GG	TT	GG	GG	CC	GG	TT
EP017	5.15		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP071	5.15		CC	CC	AA	TT	GG	GG	TT	GG	TT
EP086	5.16		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP024	5.18		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP099	5.18		CC	CC	GG	TT	GG	GG	CC	GG	TT
EP111	5.18		CC	GG	AA	TT	GG	GG	CC	AA	GG
EP176	5.19		CC	GG	GG	TT	GG	AA	CC	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP117	5.19		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP080	5.20		CC	GG	AA	TT	GG	AA	CC	GG	GG
EP021	5.20		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP154	5.20		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP114	5.21		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP149	5.21		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP171	5.21		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP038	5.22		TT	GG	AA	CC	AA	AA	CC	GG	GG
EP126	5.22		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP150	5.23		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP134	5.23		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP101	5.24		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP151	5.24		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP079	5.24		CC	GG	AA	TT	GG	AA	CC	GG	GG
EP013	5.24		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP159	5.25		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP039	5.26		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP187	5.26		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP009	5.28		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP139	5.28		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP108	5.28		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP158	5.28		TT	CC	AA	CC	GG	AA	CC	GG	TT

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP132	5.28		CC	GG	GG	CC	AA	AA	CC	GG	GG
EP116	5.29		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP020	5.29		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP185	5.30		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP123	5.30		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP029	5.31		CC	CC	GG	TT	GG	AA	CC	GG	GG
EP129	5.31		TT	GG	GG	CC	AA	AA	CC	GG	GG
EP003	5.32		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP018	5.32		CC	CC	AA	TT	GG	AA	CC	GG	GG
EP191	5.33		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP088	5.33		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP153	5.33		TT	CC	GG	TT	AA	AA	CC	AA	TT
EP031	5.35		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP184	5.36		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP085	5.39		TT	CC	AA	TT	GG	AA	CC	GG	GG
EP036	5.39		TT	CC	GG	TT	GG	GG	TT	GG	GG
EP030	5.39		TT	CC	AA	TT	GG	AA	CC	GG	GG
EP182	5.39		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP115	5.40		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP155	5.40		TT	CC	GG	CC	GG	AA	CC	GG	TT
EP022	5.40		TT	CC	AA	TT	GG	AA	CC	GG	GG
EP090	5.40		CC	CC	AA	TT	GG	GG	TT	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP083	5.41		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP186	5.42		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP050	5.42		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP197	5.43		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP125	5.43		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP195	5.44		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP131	5.45		TT	CC	GG	TT	AA	AA	CC	GG	GG
EP192	5.46		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP200	5.46		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP173	5.47		TT	CC	AA	TT	GG	AA	CC	GG	TT
EP032	5.47		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP118	5.48		CC	GG	AA	CC	GG	GG	CC	AA	GG
EP047	5.49		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP172	5.50		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP082	5.51		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP098	5.53		CC	GG	GG	CC	GG	AA	CC	GG	TT
EP143	5.53		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP041	5.53		TT	CC	AA	TT	AA	AA	CC	GG	GG
EP109	5.55		TT	GG	AA	CC	GG	GG	CC	AA	GG
EP044	5.56		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP057	5.56		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP097	5.56		CC	CC	GG	TT	GG	GG	CC	GG	TT

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP127	5.56		TT	GG	GG	CC	AA	AA	CC	GG	GG
EP170	5.59		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP189	5.59		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP142	5.59		TT	CC	GG	TT	GG	AA	CC	GG	TT
EP095	5.60		CC	CC	AA	TT	GG	AA	CC	GG	GG
EP128	5.61		TT	GG	GG	CC	AA	AA	CC	GG	GG
EP092	5.61		CC	CC	AA	TT	GG	GG	TT	GG	GG
EP081	5.61		CC	GG	AA	TT	GG	AA	CC	GG	GG
EP053	5.66		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP181	5.66		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP120	5.66		CC	GG	AA	CC	GG	AA	CC	AA	GG
EP094	5.68		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP162	5.68		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP051	5.68		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP180	5.70		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP014	5.72		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP152	5.73		TT	CC	GG	TT	GG	AA	CC	GG	GG
EP016	5.74		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP169	5.75		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP061	5.75		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP167	5.75		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP193	5.77		CC	GG	GG	TT	GG	AA	CC	GG	GG

Accession	TRN	QTL-tagging markers	IWB21309	IWB35047	IWB35568	IWB66095	IWB12589	IWB10265	IWB3767	IWB8696	IWB50513
		alleles	C/T	C/G	A/G	C/T	A/G	A/G	C/T	A/G	G/T
		chrom	4A	4B	1B	4B	1A	4B	7A	1A	3B
		cM	17.01	80.4	27.21	91.74	13.62	44.92	146.9	5.2	148.42
		-LOG10 P	3.69	3.59	3.39	3.37	3.34	3.14	3.07	3.07	2.87
		R ² (%)	7.13	6.90	6.43	6.39	6.32	5.87	5.72	5.71	5.25
		Allelic Effect	-0.43	-0.44	0.54	0.52	0.57	0.39	0.5	0.78	0.41
EP077	5.79		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP078	5.83		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP163	5.85		TT	CC	AA	TT	AA	AA	CC	AA	GG
EP075	5.90		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP179	5.92		CC	GG	GG	TT	GG	AA	CC	GG	GG
EP133	5.93		TT	GG	GG	CC	AA	AA	CC	GG	GG
EP160	5.96		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP156	5.99		CC	CC	AA	TT	AA	AA	CC	AA	GG
EP168	6.00		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP004	6.01		TT	GG	GG	TT	GG	AA	CC	GG	TT
EP034	6.07		TT	CC	AA	TT	AA	AA	CC	GG	GG
EP049	6.08		TT	CC	AA	TT	GG	AA	CC	GG	GG
EP130	6.10		TT	CC	GG	CC	GG	AA	CC	GG	GG
EP165	6.12		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP164	6.33		TT	CC	AA	CC	GG	AA	CC	GG	TT
EP046	6.36		TT	GG	AA	TT	GG	AA	CC	GG	GG
EP157	6.36		TT	CC	AA	CC	GG	GG	CC	GG	TT
EP033	6.75		TT	GG	AA	CC	AA	AA	CC	AA	GG
SNP allele frequency (-ve effect)			CC	CC	GG	TT	GG	GG	TT	GG	TT
			0.47	0.47	0.42	0.76	0.92	0.28	0.11	0.84	0.25
SNP allele frequency (+ve effect)			TT	GG	AA	CC	AA	AA	CC	AA	GG
			0.53	0.53	0.58	0.24	0.08	0.72	0.89	0.16	0.75

Appendix Table 7. Allelic distribution for individual root weight (IRW) QTL-tagging SNPs in the Ethiopian durum wheat panel.

Accessions are listed by IRW.

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP060	5.94		TT	GG	TT	TT	CC	GG	TT	AA	TT	CC
EP049	7.79		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP147	7.86		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP022	7.88		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP048	7.95		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP059	7.99		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP182	8.17		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP012	8.18		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP150	8.20		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP018	8.33		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP041	8.48		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP087	8.51		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP132	8.52		TT	GG	TT	CC	CC	AA	TT	AA	TT	CC
EP078	8.57		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP160	8.82		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP034	8.85		TT	GG	TT	CC	CC	AA	TT	AA	GG	CC
EP085	8.85		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP003	8.91		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP183	9.00		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP157	9.00		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP158	9.02		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP042	9.04		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP188	9.08		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP193	9.10		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP190	9.19		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP198	9.24		TT	GG	TT	CC	CC	AA	TT	AA	TT	CC
EP029	9.29		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP061	9.33		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP179	9.33		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP149	9.34		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP036	9.35		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP058	9.38		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP181	9.39		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP172	9.39		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP002	9.42		TT	GG	TT	TT	CC	AA	TT	AA	TT	CC
EP142	9.43		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP019	9.43		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP026	9.47		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP090	9.47		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP033	9.48		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP025	9.49		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP032	9.55		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP014	9.56		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP052	9.60		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP169	9.62		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP096	9.66		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP031	9.71		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP079	9.75		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP037	9.78		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP039	9.81		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP187	9.81		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP197	9.81		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP133	9.86		TT	GG	TT	CC	CC	AA	TT	AA	GG	CC
EP064	9.87		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP020	9.88		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP189	9.89		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP128	9.91		TT	GG	TT	CC	CC	AA	TT	AA	GG	CC
EP001	9.92		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP030	9.94		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP062	9.96		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP093	9.97		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP195	9.98		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP154	10.02		TT	GG	TT	CC	CC	GG	GG	AA	TT	AA
EP009	10.04		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP185	10.07		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP192	10.09		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP091	10.10		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP083	10.10		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP168	10.11		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP170	10.12		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP005	10.16		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP180	10.22		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP013	10.23		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP074	10.24		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP191	10.25		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP063	10.26		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP082	10.28		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP138	10.29		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP075	10.35		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP092	10.45		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP194	10.49		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP072	10.52		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP159	10.55		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP080	10.56		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP044	10.57		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP028	10.63		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP089	10.66		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP151	10.73		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP084	10.80		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP051	10.80		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP186	10.81		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP021	10.88		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP184	10.90		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP068	10.93		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP050	10.99		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP053	10.99		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP127	11.00		TT	GG	TT	CC	CC	AA	TT	AA	GG	CC
EP163	11.00		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP167	11.05		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP165	11.06		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP076	11.08		TT	GG	TT	CC	CC	GG	TT	AA	GG	AA
EP153	11.08		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP086	11.09		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP043	11.27		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP071	11.29		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP129	11.30		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP023	11.30		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP171	11.31		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP102	11.31		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP015	11.35		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP017	11.36		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP162	11.37		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP024	11.39		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP057	11.42		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP175	11.42		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP145	11.43		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP176	11.48		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP056	11.49		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP134	11.50		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP199	11.50		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP046	11.51		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP136	11.55		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP070	11.61		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP146	11.69		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP004	11.69		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP054	11.71		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP069	11.74		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP067	11.76		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP164	11.76		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP088	11.81		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP141	11.81		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP055	11.82		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP144	11.83		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP047	11.83		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP008	11.88		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP099	11.91		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP140	11.98		TT	GG	TT	CC	CC	AA	TT	AA	TT	CC
EP137	12.03		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP016	12.32		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP143	12.44		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP166	12.44		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP011	12.50		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP094	12.61		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP038	12.69		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP081	12.70		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP045	12.76		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP196	12.76		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP065	12.79		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP200	12.79		TT	GG	TT	TT	CC	AA	TT	GG	GG	CC
EP077	12.80		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP095	12.81		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP131	12.84		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC

Accession	IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
		alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
		chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
		cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
		-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
		R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
		Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP097	12.98		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP152	13.17		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP098	13.25		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP006	13.42		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP173	13.57		TT	GG	TT	CC	CC	GG	TT	AA	TT	CC
EP156	13.57		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP139	13.77		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP174	13.80		CC	AA	TT	TT	CC	GG	GG	GG	GG	AA
EP124	13.83		CC	GG	TT	TT	CC	GG	GG	GG	GG	CC
EP010	13.89		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP105	13.94		CC	AA	CC	CC	AA	GG	GG	GG	TT	AA
EP066	14.28		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP108	14.39		CC	AA	CC	TT	CC	GG	TT	GG	GG	AA
EP155	14.39		TT	GG	TT	TT	CC	GG	TT	AA	GG	CC
EP130	14.58		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP007	14.61		TT	GG	TT	CC	CC	GG	TT	AA	GG	CC
EP121	16.08		CC	AA	CC	TT	AA	GG	TT	AA	GG	AA
EP135	16.71		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC
EP118	16.72		CC	AA	TT	CC	CC	GG	GG	GG	TT	AA
EP123	16.82		CC	AA	CC	CC	CC	GG	GG	GG	TT	AA
EP109	17.13		CC	GG	CC	TT	AA	GG	TT	GG	GG	AA
EP100	17.23		TT	GG	TT	TT	CC	AA	TT	AA	GG	CC

Accession IRW	QTL-tagging markers	IWA3196	IWB29332	IWB73456	IWB11841	IWB70122	IWB60732	IWA332	IWB35797	IWB45867	IWB72335
	alleles	C/T	A/G	C/T	C/T	A/C	A/G	G/T	A/G	G/T	A/C
	chrom	5A	2B	6B	7A	5B	1B	5B	7B	7A	7B
	cM	16.83	160.51	90.33	94.72	40.39	33.75	16.73	112.52	91.82	58.34
	-LOG10 P	4.06	3.48	3.34	3.16	3.15	3.10	3.00	2.94	2.89	2.75
	R ² (%)	8.03	6.675	6.338	5.944	5.919	5.803	5.563	5.435	5.331	5.001
	Allelic Effect	7.54	4.5	2.94	-1.43	2.81	1.7	-2.96	-2.77	1.55	-1.58
EP104	17.39	CC	AA	CC	TT	CC	GG	GG	AA	GG	CC
EP111	17.49	CC	AA	CC	CC	AA	GG	GG	GG	GG	AA
EP117	17.62	CC	AA	TT	TT	AA	GG	GG	GG	GG	AA
EP106	17.63	CC	AA	CC	TT	CC	GG	GG	GG	GG	CC
EP126	17.67	CC	AA	TT	CC	AA	GG	GG	GG	TT	CC
EP125	17.74	CC	AA	CC	TT	CC	GG	GG	GG	GG	CC
EP122	18.01	CC	AA	CC	TT	AA	GG	GG	GG	GG	AA
EP107	18.15	CC	AA	CC	TT	AA	GG	TT	GG	GG	AA
EP112	18.52	CC	AA	CC	TT	CC	GG	GG	AA	GG	CC
EP113	18.99	CC	AA	CC	CC	AA	GG	GG	GG	GG	AA
EP101	19.21	CC	AA	TT	TT	AA	GG	TT	GG	GG	AA
EP114	19.24	CC	AA	CC	TT	AA	GG	TT	AA	GG	AA
EP119	19.40	CC	AA	CC	TT	AA	GG	TT	GG	GG	AA
EP120	19.46	CC	AA	CC	TT	AA	GG	TT	GG	GG	AA
EP110	19.99	CC	AA	CC	TT	AA	GG	TT	GG	TT	CC
EP103	20.00	CC	AA	CC	CC	AA	GG	TT	GG	GG	AA
EP115	21.31	CC	AA	CC	TT	CC	GG	TT	GG	GG	CC
EP116	21.48	CC	AA	CC	TT	AA	GG	TT	GG	GG	AA
SNP allele frequency (-ve effect)		TT	GG	TT	CC	CC	GG	GG	AA	TT	AA
		0.86	0.88	0.1	0.34	0.92	0.78	0.08	0.88	0.14	0.1
SNP allele frequency (+ve effect)		CC	AA	CC	TT	AA	AA	TT	GG	GG	CC
		0.14	0.12	0.9	0.66	0.08	0.22	0.92	0.12	0.86	0.9

Appendix Table 8. Phenotypic mean values for grain shape and color related traits in 192 Ethiopian durum wheat accessions.

ID	GL	GW	L*	a*	b*
EP001	8.03	3.09	64.5	7.45	14.54
EP002	7.99	3.26	63.13	8.49	15.84
EP003	6.56	2.76	50.36	11.19	15.23
EP004	8.17	3.06	58.3	8.66	15.89
EP005	7.8	3.35	63.4	8.01	20.29
EP006	7.49	2.84	50.9	11.61	16.36
EP007	8.09	3.28	61.73	8.46	16.96
EP008	7.8	3.37	61.6	8.63	16.45
EP009	7.33	3.03	58.82	9.18	15.36
EP010	6.68	2.69	47.4	11.97	15.35
EP011	7.29	2.85	46.44	12.84	15.2
EP012	7.22	3.13	63.67	7.67	19.09
EP013	7.65	3.35	64.16	7.85	18.31
EP014	7.42	3.33	61.58	8.33	18.4
EP015	7.4	3.13	61.87	8.63	16.03
EP016	7.51	3.12	61.94	8.86	17.68
EP017	7.22	3.21	64.03	7.7	19.18
EP018	7.01	3.06	55.91	10.06	16.77
EP019	7.6	3.23	62.44	8.48	16.38
EP020	7.29	3.28	63	7.78	18.99
EP021	6.99	2.8	58.42	9.55	15.29
EP022	8.05	3.25	65.52	7.49	16.89
EP023	7.45	3.06	61.87	8.79	16.32
EP024	8	3.31	62.21	8.62	16.82
EP025	8.03	3.39	61.62	7.93	14.74
EP026	7.96	2.98	44.77	12.49	14.88
EP028	6.44	2.71	45.85	12.19	14.65
EP029	8.24	3.57	61.5	8.03	18.56
EP030	7.73	3.04	61.53	8.54	16.24
EP031	7.86	3.45	62.32	8.13	18.15
EP032	7.72	3.07	59.43	8.98	15.89
EP033	7.43	3.38	60.52	8.8	16.19
EP034	7.98	3.15	60.76	8.41	15.44
EP036	7.65	3.1	61.2	8.4	15.36
EP037	7	2.97	50.3	12.5	17.83
EP038	6.65	2.73	47.13	12.57	16.14
EP039	7.58	3.14	61.42	8.85	16.34
EP041	7.8	3.02	60.83	8.66	15.31
EP042	7.64	3.1	61.07	8.52	15.37

ID	GL	GW	L*	a*	b*
EP043	7.7	3	63.79	7.61	17.52
EP044	7.95	3	59.6	8.73	15.73
EP045	7.89	2.86	60.85	9.18	16.86
EP046	8.37	2.96	60.76	9.04	16.25
EP047	8.1	3.06	60.36	8.88	15.79
EP048	7.13	2.54	50.4	11.01	13.82
EP049	7.42	3.06	62.19	8.8	16.73
EP050	7.75	2.94	53.67	10.97	15.84
EP051	7.39	2.96	52.51	11.51	16.47
EP052	7.23	3.19	60.85	8.78	15.97
EP053	7.19	2.9	54.74	10.22	15.32
EP054	7.27	2.92	54.7	10.06	15.61
EP055	7.38	3.09	51.37	11.79	17.38
EP056	7.46	2.89	59.02	9.2	16.28
EP057	7.06	3.21	59.62	8.96	15.4
EP058	7.58	2.9	62.32	8.76	16.66
EP059	7.09	3.11	61.26	8.5	15.47
EP060	7.4	2.95	63.44	8.15	14.54
EP061	7.31	2.94	50.03	12	15.47
EP062	7.24	2.64	46.34	12.22	14.6
EP063	7.22	2.54	47.08	11.56	13.37
EP064	7.23	2.53	46.93	12.22	13.85
EP065	6.58	2.52	46.29	11.97	13.7
EP066	7.27	2.67	47.39	11.74	14.4
EP067	7	2.6	46.93	11.61	13.03
EP068	7.48	2.79	48.59	12	15.22
EP069	7.09	2.81	47.51	12.44	15.36
EP070	6.67	2.85	46.23	12.77	14.42
EP071	6.95	2.77	45.76	12.74	14.13
EP072	7.49	2.93	48.22	12.24	15.42
EP074	7.09	2.63	50.8	11.59	14.72
EP075	7.5	2.97	60.94	8.93	16.66
EP076	7.17	2.94	59.25	9.41	15.62
EP077	7.65	3.29	61.93	8.09	18.39
EP078	7.38	2.73	51.56	11.42	15.43
EP079	7.21	2.74	50.58	11.76	15.42
EP080	7.2	2.73	50.26	11.75	15.34
EP081	6.84	2.67	49.27	12.2	16.34
EP082	8.23	3.25	61.98	8.66	16.76
EP083	7.69	3	61.05	8.95	16.23
EP084	7.31	3.09	60.91	9.04	16.04
EP085	7.36	3.21	62.92	8.59	16.59
EP086	7.55	3.11	65.2	7.63	17.92
EP087	7.49	2.76	52.67	11.12	14.61
EP088	6.25	2.75	49.37	11.57	14.77

ID	GL	GW	L*	a*	b*
EP089	7.02	2.89	48.44	11.87	14.19
EP090	6.65	2.81	47.57	12.3	14.71
EP091	6.45	2.8	47.34	12.42	14.45
EP092	6.81	2.87	48.82	11.6	14.56
EP093	6.73	2.79	50.28	11.32	14.29
EP094	7.58	3.12	63.45	8.35	16.17
EP095	7.85	3.03	63.34	7.74	14.04
EP096	7.48	3.06	63.47	8.17	18.48
EP097	7.06	2.73	43.53	13.06	11.06
EP098	6.36	2.56	45.94	12.23	11.6
EP099	7.31	2.66	45.57	12.19	11.15
EP100	7.64	3.13	61.55	8.87	15.94
EP101	7.82	3.2	59	8.35	19.68
EP102	8.08	3.26	63.63	7.86	13.83
EP103	7.6	3.35	64.02	7.17	17.92
EP104	7.74	3.17	60.81	7.62	18.09
EP105	7.47	2.98	67.43	8.35	19.05
EP106	7.96	3.32	61.9	7.23	18.38
EP107	7.94	3.11	60.19	7.83	19.32
EP108	7.51	3.32	61.68	8.11	18.33
EP109	8.59	3.14	64.93	7.43	18.54
EP110	7.4	3.28	63.48	7.27	17.85
EP111	7.62	3.34	62.35	7.8	19.05
EP112	8.01	3.19	59.9	7.67	17.9
EP113	8.27	3.21	60.24	8.09	17.92
EP114	7.52	3.11	59.77	8.31	18.94
EP115	8.05	3.32	62.11	7.23	17.15
EP116	7.68	3.1	60.18	8.29	19.36
EP117	8.15	3.33	58.52	8.34	19.37
EP118	7.94	3.3	59.32	7.98	19.23
EP119	7.43	3.15	61.41	7.57	20.67
EP120	7.87	3.15	60.78	7.73	20.1
EP121	7.47	3.15	62.31	7.81	20.89
EP122	8.01	3.32	60.75	7.82	18.88
EP123	8.03	3.33	60.48	7.65	18.79
EP124	7.69	3.39	60.51	7.87	19.65
EP125	8.1	3.3	60.16	7.61	18.67
EP126	8.26	3.34	62.97	7.4	17.91
EP127	8.21	2.77	47.1	11.69	12.55
EP128	8.54	2.92	47.49	11.98	13.36
EP129	8.47	2.85	54.23	10.24	15.04
EP130	8.7	2.74	47.76	12.15	12.34
EP131	7.85	2.77	47.79	11.73	11.93
EP132	8.18	2.8	52.89	10.2	13.52
EP133	8.37	2.71	48.21	11.81	12.69

ID	GL	GW	L*	a*	b*
EP134	7.38	3.35	63.76	7.92	18.34
EP135	7.83	3.37	66.92	7.04	17.41
EP136	7.73	3.39	67.07	7.24	17.91
EP137	7.65	3.42	67.28	7.2	18.12
EP138	7.29	3.32	64.37	7.89	18.05
EP139	7.43	3.38	64.22	7.97	17.81
EP140	7.78	3.31	66.04	7.49	19
EP141	7.38	3.34	64.28	8.04	19.21
EP142	7.35	3.27	62.87	8.16	14.82
EP143	7.91	3.38	67.03	7.16	17.65
EP144	8.15	3.07	60.02	9.14	16.03
EP145	7.76	3.42	66.93	7.38	17.7
EP146	7.83	3.4	65.02	7.78	19.03
EP147	7.71	3.24	67.25	7.06	18.1
EP149	7.53	3.4	66.89	7.41	17.86
EP150	7.51	3.32	67.78	7.16	18.18
EP151	7.37	3.35	64.78	8.14	20.13
EP152	8.05	3.46	66.62	7.46	18.35
EP153	8.51	3.29	58.59	9.19	15.79
EP154	6.94	2.91	45.33	12.46	12.43
EP155	7.73	3.49	64.54	7.72	19.45
EP156	7.91	3.26	63.79	7.66	17.75
EP157	8.1	3.42	63.28	7.54	17.65
EP158	7.68	3.21	65.36	7.5	17.99
EP159	7.64	3.32	63.05	7.76	18.08
EP160	7.63	3.25	64.43	7.57	17.92
EP162	7.6	3.22	62.17	8.12	19.24
EP163	8.31	2.9	61.04	8.32	14.73
EP164	7.92	3.35	64.09	8.13	18.68
EP165	7.91	3.35	64.57	7.88	18.53
EP166	8	3.16	61.63	8.81	16.91
EP167	7.65	3.23	62.19	8.1	18.44
EP168	7.5	3.24	64.35	8.07	18.21
EP169	7.85	3.3	64.4	7.91	18.59
EP170	7.85	3.29	64.81	7.82	18.58
EP171	8.01	3.38	64.22	7.95	17.91
EP172	7.6	3.38	64.21	8.14	18.58
EP173	7.48	3.43	63.96	7.93	18.92
EP174	7.53	3.42	59.15	8.31	20.27
EP175	6.71	2.65	45.29	11.83	13.05
EP176	6.4	2.6	44.72	12.06	12.8
EP179	6.54	2.61	46.68	12.57	11.41
EP180	6.7	2.71	48.13	12.33	12.57
EP181	7.22	2.83	44.28	13.18	11.65
EP182	6.91	2.69	46.15	13.2	12.11

ID	GL	GW	L*	a*	b*
EP183	7.07	2.73	46.57	12.77	12.45
EP184	7.36	2.82	47.88	12.58	12.41
EP185	6.8	2.81	46.94	12.4	12.99
EP186	7.03	2.61	47.65	12.63	12.81
EP187	6.67	2.67	46.87	12.76	12.74
EP188	6.94	2.69	46.75	12.37	11.78
EP189	7.3	2.77	46.57	12.44	11.11
EP190	6.71	2.68	48.32	12.46	11.44
EP191	6.61	2.67	44.74	13.09	11.65
EP192	6.77	2.72	44.58	12.98	11.07
EP193	6.65	2.68	46.51	12.48	12.33
EP194	5.99	2.44	44.23	13.11	11.31
EP195	6.86	2.7	47.21	12.88	12.2
EP196	7.3	2.75	47.37	12.06	13.25
EP197	6.77	2.81	46.73	12.42	12.62
EP198	7.05	3.23	64.29	8.54	15.81
EP199	7.96	3.41	66.25	6.64	17.32
EP200	7.87	3.5	66.54	6.53	17.44

Appendix Table 9. List of all identified QTLs for kernel shape and color traits in Ethiopian durum wheat.

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
a*	IWB57868	1A	1.74	2.53	4.6	0	3.99	A	-0.83	65	G	0	127
a*	IWB8286	2A	117.05	2.98	5.6	114.8	119.3	C	1.38	43	T	0	149
a*	IWB72154	2A	136.04	5.39	11.4	133.79	138.29	C	1.36	104	T	0	88
a*	IWA3196	5A	16.83	2.81	5.2	14.58	19.08	C	-4.07	26	T	0	166
a*	IWB66972	7A	113.61	2.81	5.2	111.36	115.86	A	-1.58	172	G	0	20
L*	IWB65551	1A	87	3.17	6.0	84.75	89.25	C	5.19	115	T	0	77
L*	IWB8286	2A	117.05	3.30	6.3	114.8	119.3	C	-5.35	43	T	0	149
L*	IWB72154	2A	136.04	5.23	11.0	133.79	138.29	C	-4.96	104	T	0	88
L*	IWB7271	5A	84.72	2.67	4.9	82.47	86.97	A	1.62	33	G	0	159
L*	IWB70454	6A	117.1	2.65	4.8	114.85	119.35	A	-4.59	111	G	0	81
L*	IWB66972	7A	113.61	2.76	5.1	111.36	115.86	A	5.85	172	G	0	20
L*	IWB72494	7A	143.19	3.14	5.9	140.94	145.44	G	7.48	167	T	0	25
L*	IWB62029	7B	165.05	3.26	6.2	162.8	167.3	C	6.66	182	T	0	10
b*	IWB11958	1B	115.74	3.40	6.3	113.49	117.99	C	1.32	147	T	0	45
b*	IWB57773	2A	108.99	2.89	5.2	106.74	111.24	A	3.63	25	G	0	167
b*	IWB27216	2B	100.93	2.79	5.0	98.68	103.18	A	-1.83	180	G	0	12
b*	IWB11992	3A	141.52	3.08	5.6	139.27	143.77	A	1.46	61	G	0	131
b*	IWB73411	4B	39.47	3.40	6.3	37.22	41.72	C	-1.45	22	T	0	170
b*	IWA3196	5A	16.83	3.10	5.7	14.58	19.08	C	4.66	26	T	0	166
b*	IWB75144	6A	75.23	2.93	5.3	72.98	77.48	C	3.35	162	T	0	30
b*	IWB34768	7B	67.34	3.14	5.8	65.09	69.59	C	1.28	55	T	0	137
GL	IWB27591	1A	20.72	2.68	5.0	18.47	22.97	A	-0.40	149	C	0	43
GL	IWB27914	1A	62.81	2.79	5.3	60.56	65.06	G	-0.92	30	T	0	162
GL	IWB24876	1B	0.02	2.55	4.7	0	2.27	C	0.29	137	T	0	55

Trait*	Marker	Chr	Position (cM)	P (-log10)	R ² (%)	Significance Interval left (cM)	Significance Interval right (cM)	Allele (SNP base)	Effect	Allele count (No.)	Allele (SNP base)	Effect	Allele count (No.)
GL	IWB25023	1B	35.89	2.80	5.3	33.64	38.14	C	0.48	55	T	0	137
GL	IWB50027	1B	87.82	2.61	4.9	85.57	90.07	A	0.38	135	G	0	57
GL	IWB72779	2A	66.33	2.62	4.9	64.08	68.58	A	-0.93	26	C	0	166
GL	IWB3865	2B	108.92	3.14	6.1	106.67	111.17	C	-0.37	102	T	0	90
GL	IWB71698	4A	171.01	2.96	5.7	168.76	173.26	C	-0.67	25	T	0	167
GL	IWB9672	4B	66.43	3.42	6.8	64.18	68.68	C	0.67	38	T	0	154
GL	IWA3196	5A	16.83	2.60	4.9	14.58	19.08	C	1.25	26	T	0	166
GL	IWB43493	5A	72.73	3.01	5.8	70.48	74.98	C	-0.45	50	T	0	142
GL	IWB67412	6A	1.06	3.02	5.8	0	3.31	A	-0.39	141	G	0	51
GL	IWB12715	6A	32.71	2.95	5.7	30.46	34.96	C	0.37	160	T	0	32
GL	IWB7484	7A	68.71	2.66	5.0	66.46	70.96	A	-0.39	86	C	0	106
GL	IWA2568	7B	20.75	3.06	5.9	18.5	23	A	-0.55	159	G	0	33
GW	IWB46763	2A	114.7	2.64	4.7	112.45	116.95	A	0.26	180	G	0	12
GW	IWB72154	2A	136.04	3.59	6.8	133.79	138.29	C	-0.15	104	T	0	88
GW	IWB23912	2A	208.76	3.01	5.5	206.51	211.01	C	-0.32	31	T	0	161
GW	IWB65507	3B	126.23	2.82	5.0	123.98	128.48	A	-0.30	159	G	0	33
GW	IWB72936	4B	39.45	2.76	4.9	37.2	41.7	A	-0.14	41	G	0	151
GW	IWB43493	5A	72.73	2.84	5.1	70.48	74.98	C	-0.19	50	T	0	142
GW	IWB46350	5A	84.77	3.52	6.6	82.52	87.02	A	-0.20	114	G	0	78
GW	IWB20043	6B	85.2	2.74	4.9	82.95	87.45	G	-0.11	104	T	0	88
GW	IWB36189	7B	66.36	3.06	5.6	64.11	68.61	A	-0.15	137	G	0	55
GW	IWB68837	7B	108.1	2.65	4.7	105.85	110.35	A	-0.15	157	G	0	35

Appendix Table 10. Allelic distribution for grain length (GL) QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by GL.

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP194	5.99	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP088	6.25	AA	TT	TT	TT	GG	CC	TT	TT	TT	TT	TT	TT	CC
EP098	6.36	AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP176	6.4	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP028	6.44	AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC	AA
EP091	6.45	AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	TT	CC
EP179	6.54	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP003	6.56	AA	GG	CC	TT	GG	CC	TT	TT	TT	TT	TT	CC	CC
EP065	6.58	AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP191	6.61	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP038	6.65	AA	GG	CC	TT	AA	CC	CC	CC	TT	TT	TT	CC	CC
EP090	6.65	AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	TT	CC
EP193	6.65	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP070	6.67	AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	TT	CC
EP187	6.67	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP010	6.68	AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	TT	CC
EP180	6.7	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP175	6.71	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP190	6.71	AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	TT	AA
EP093	6.73	AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	TT	CC

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP192	6.77		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP197	6.77		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP185	6.8		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP092	6.81		AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP081	6.84		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP195	6.86		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP182	6.91		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP154	6.94		AA	GG	TT	TT	AA	AA	CC	CC	TT	TT	CC	AA
EP188	6.94		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP071	6.95		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP021	6.99		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP037	7		AA	TT	CC	CC	GG	CC	TT	TT	TT	TT	TT	CC
EP067	7		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP018	7.01		AA	TT	TT	TT	GG	CC	TT	TT	TT	TT	TT	CC
EP089	7.02		AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP186	7.03		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP198	7.05		CC	TT	TT	CC	AA	CC	CC	TT	TT	TT	CC	AA
EP057	7.06		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP097	7.06		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP183	7.07		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP059	7.09		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP069	7.09		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP074	7.09		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP048	7.13		CC	TT	TT	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP076	7.17		AA	GG	CC	TT	GG	AA	TT	CC	TT	TT	CC	AA
EP053	7.19		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP080	7.2		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP079	7.21		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP012	7.22		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP017	7.22		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP063	7.22		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP181	7.22		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP052	7.23		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP064	7.23		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP062	7.24		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP054	7.27		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP066	7.27		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP011	7.29		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP020	7.29		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP138	7.29		CC	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP189	7.3		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP196	7.3		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP061	7.31		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP084	7.31		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP099	7.31		AA	TT	TT	CC	GG	CC	TT	TT	TT	TT	TT	AA
EP009	7.33		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP142	7.35		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	AA
EP085	7.36		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP184	7.36		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	AA
EP151	7.37		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	AA
EP055	7.38		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP078	7.38		AA	TT	TT	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP134	7.38		CC	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP141	7.38		CC	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP051	7.39		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	CC	CC
EP015	7.4		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP060	7.4		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP110	7.4		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP014	7.42		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP049	7.42		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	CC	CC
EP033	7.43		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP119	7.43		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP139	7.43		CC	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP023	7.45		AA	TT	CC	CC	AA	CC	CC	TT	TT	TT	CC	CC
EP056	7.46		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	CC
EP105	7.47		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP121	7.47		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP068	7.48		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP096	7.48		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP173	7.48		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	AA
EP006	7.49		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP072	7.49		AA	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP087	7.49		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP075	7.5		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP168	7.5		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP016	7.51		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP108	7.51		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP150	7.51		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP114	7.52		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP149	7.53		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP174	7.53		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP086	7.55		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP039	7.58		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP058	7.58		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP094	7.58		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP019	7.6		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP103	7.6		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP162	7.6		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP172	7.6		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP111	7.62		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP160	7.63		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP042	7.64		AA	TT	CC	CC	GG	CC	TT	TT	TT	TT	TT	CC
EP100	7.64		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	CC	CC
EP159	7.64		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP013	7.65		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP036	7.65		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP077	7.65		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	CC
EP137	7.65		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP167	7.65		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP116	7.68		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP158	7.68		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP083	7.69		AA	TT	CC	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP124	7.69		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	CC
EP043	7.7		AA	TT	CC	TT	GG	CC	TT	TT	TT	TT	TT	CC
EP147	7.71		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP032	7.72		AA	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	CC
EP030	7.73		AA	TT	TT	CC	AA	CC	CC	TT	TT	TT	TT	AA
EP136	7.73		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP155	7.73		CC	TT	TT	CC	AA	CC	CC	TT	TT	TT	TT	AA
EP104	7.74		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP050	7.75		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	CC	CC
EP145	7.76		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP140	7.78		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP005	7.8		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP008	7.8		CC	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP041	7.8		AA	TT	CC	CC	GG	CC	TT	TT	TT	TT	TT	CC
EP101	7.82		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP135	7.83		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP146	7.83		AA	TT	CC	CC	AA	CC	CC	TT	TT	TT	TT	CC
EP095	7.85		CC	TT	TT	CC	AA	CC	CC	TT	TT	TT	TT	CC
EP131	7.85		CC	TT	TT	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP169	7.85		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP170	7.85		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP031	7.86		CC	TT	TT	TT	AA	CC	CC	TT	TT	TT	TT	AA
EP120	7.87		AA	GG	CC	TT	AA	AA	CC	TT	CC	CC	CC	CC
EP200	7.87		CC	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP045	7.89		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP143	7.91		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP156	7.91		CC	TT	CC	CC	AA	CC	TT	TT	TT	TT	CC	CC
EP165	7.91		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP164	7.92		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP107	7.94		AA	GG	CC	TT	AA	AA	CC	TT	CC	CC	CC	AA

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP118	7.94		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP044	7.95		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP026	7.96		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP106	7.96		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP199	7.96		CC	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP034	7.98		AA	TT	CC	CC	GG	CC	TT	TT	TT	TT	TT	CC
EP002	7.99		CC	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP024	8		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP166	8		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	CC	CC
EP112	8.01		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP122	8.01		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP171	8.01		CC	TT	CC	TT	AA	CC	CC	TT	TT	TT	CC	AA
EP001	8.03		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP025	8.03		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP123	8.03		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP022	8.05		CC	TT	CC	TT	GG	CC	CC	TT	TT	TT	TT	CC
EP115	8.05		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP152	8.05		AA	TT	TT	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP102	8.08		CC	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP007	8.09		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP047	8.1		CC	TT	CC	TT	AA	CC	TT	TT	CC	TT	TT	CC
EP125	8.1		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA

Accession	GL	QTL-tagging markers	IWB27591	IWB27914	IWB24876	IWB25023	IWB50027	IWB72779	IWB3865	IWB71698	IWB9672	IWA3196	IWB43493	IWB7484
		alleles	A/C	G/T	C/T	C/T	A/G	A/C	C/T	C/T	C/T	C/T	C/T	A/C
		chrom	1A	1A	1B	1B	1B	2A	2B	4A	4B	5A	5A	7A
		cM	20.72	62.81	0.02	35.89	87.82	66.33	108.92	171.01	66.43	16.83	72.73	68.71
		-LOG10 P	2.68	2.79	2.55	2.80	2.61	2.62	3.14	2.96	3.42	2.60	3.01	2.66
		R ² (%)	5.0	5.3	4.7	5.3	4.9	4.9	6.1	5.7	6.8	4.9	5.8	5.0
		Allelic Effect	-0.40	-0.92	0.29	0.48	0.38	-0.93	-0.37	-0.67	0.67	1.25	-0.45	-0.39
EP157	8.1		CC	TT	CC	TT	GG	CC	CC	TT	TT	TT	CC	CC
EP117	8.15		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP144	8.15		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP004	8.17		AA	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	AA
EP132	8.18		CC	TT	TT	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP127	8.21		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP082	8.23		AA	TT	CC	TT	AA	CC	TT	TT	TT	TT	TT	CC
EP029	8.24		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP126	8.26		AA	GG	CC	TT	AA	CC	CC	TT	CC	CC	CC	AA
EP113	8.27		AA	GG	CC	TT	AA	AA	CC	CC	CC	CC	CC	AA
EP163	8.31		CC	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP046	8.37		CC	TT	CC	TT	AA	CC	TT	TT	CC	TT	TT	CC
EP133	8.37		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP129	8.47		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP153	8.51		CC	TT	CC	CC	AA	CC	TT	TT	TT	TT	TT	CC
EP128	8.54		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
EP109	8.59		AA	GG	CC	TT	AA	CC	CC	TT	CC	CC	CC	CC
EP130	8.7		CC	TT	CC	CC	AA	CC	TT	TT	CC	TT	TT	CC
SNP allele frequency (-ve effect)			AA	GG	TT	TT	GG	AA	CC	CC	TT	TT	CC	AA
			0.78	0.16	0.28	0.71	0.29	0.14	0.53	0.13	0.80	0.86	0.26	0.45
SNP allele frequency (+ve effect)			CC	TT	CC	CC	AA	CC	TT	TT	CC	CC	TT	CC
			0.22	0.84	0.72	0.29	0.71	0.86	0.47	0.87	0.20	0.14	0.74	0.55

Appendix Table 11. Allelic distribution for Grain width (GW) QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by GW.

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP194	2.44		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP065	2.52		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP064	2.53		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP048	2.54		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP063	2.54		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP098	2.56		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP067	2.6		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP176	2.6		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP179	2.61		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP186	2.61		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP074	2.63		AA	CC	TT	AA	GG	TT	AA	TT	AA	AA
EP062	2.64		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP175	2.65		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP099	2.66		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP066	2.67		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP081	2.67		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP187	2.67		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP191	2.67		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP190	2.68		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP193	2.68		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP010	2.69		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP182	2.69		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP188	2.69		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP195	2.7		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP028	2.71		GG	TT	CC	AA	AA	CC	AA	GG	GG	AA
EP133	2.71		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP180	2.71		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP192	2.72		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP038	2.73		AA	CC	TT	AA	AA	CC	AA	TT	AA	AA
EP078	2.73		AA	CC	TT	AA	GG	TT	AA	TT	AA	AA
EP080	2.73		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP097	2.73		AA	CC	TT	AA	AA	TT	AA	TT	GG	AA
EP183	2.73		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP079	2.74		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP130	2.74		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP088	2.75		AA	CC	TT	AA	GG	TT	AA	GG	GG	AA
EP196	2.75		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP003	2.76		AA	CC	TT	AA	AA	CC	AA	GG	AA	AA
EP087	2.76		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP071	2.77		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP127	2.77		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP131	2.77		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP189	2.77		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP068	2.79		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP093	2.79		AA	CC	TT	AA	GG	TT	AA	TT	AA	AA
EP021	2.8		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP091	2.8		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP132	2.8		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP069	2.81		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP090	2.81		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP185	2.81		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP197	2.81		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP184	2.82		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP181	2.83		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP006	2.84		AA	CC	TT	AA	GG	TT	AA	TT	AA	GG
EP011	2.85		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP070	2.85		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP129	2.85		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP045	2.86		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP092	2.87		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP056	2.89		AA	TT	TT	AA	GG	CC	AA	GG	AA	AA
EP089	2.89		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP053	2.9		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP058	2.9		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP163	2.9		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP154	2.91		AA	CC	CC	GG	AA	CC	GG	TT	AA	AA
EP054	2.92		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP128	2.92		AA	CC	TT	AA	AA	TT	AA	GG	AA	AA
EP072	2.93		AA	CC	TT	AA	GG	TT	AA	GG	AA	AA
EP050	2.94		AA	CC	TT	AA	GG	CC	AA	GG	AA	AA
EP061	2.94		AA	TT	TT	AA	GG	TT	AA	GG	AA	GG
EP076	2.94		AA	CC	CC	AA	AA	CC	GG	GG	AA	AA
EP060	2.95		AA	CC	TT	AA	GG	TT	GG	GG	GG	AA
EP046	2.96		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP051	2.96		AA	CC	TT	AA	GG	CC	AA	GG	AA	AA
EP037	2.97		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP075	2.97		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP026	2.98		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP105	2.98		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP043	3		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP044	3		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP083	3		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP041	3.02		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP009	3.03		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP095	3.03		AA	TT	TT	AA	GG	TT	GG	GG	GG	AA
EP030	3.04		AA	TT	CC	AA	GG	TT	AA	GG	GG	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP004	3.06		AA	CC	TT	AA	GG	TT	GG	GG	AA	AA
EP018	3.06		AA	CC	TT	AA	GG	TT	AA	GG	GG	AA
EP023	3.06		AA	CC	TT	AA	GG	CC	AA	TT	AA	AA
EP047	3.06		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP049	3.06		AA	TT	TT	AA	GG	CC	AA	GG	GG	AA
EP096	3.06		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP032	3.07		AA	TT	TT	AA	GG	TT	AA	GG	AA	GG
EP144	3.07		AA	CC	TT	AA	GG	TT	GG	GG	AA	AA
EP001	3.09		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP055	3.09		AA	CC	TT	AA	GG	TT	GG	GG	AA	AA
EP084	3.09		AA	TT	TT	AA	GG	TT	AA	TT	AA	GG
EP036	3.1		AA	CC	TT	AA	GG	TT	GG	GG	AA	AA
EP042	3.1		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP116	3.1		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP059	3.11		AA	TT	TT	AA	GG	TT	GG	TT	AA	GG
EP086	3.11		AA	TT	TT	AA	GG	TT	AA	GG	AA	GG
EP107	3.11		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP114	3.11		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP016	3.12		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP094	3.12		AA	TT	TT	AA	GG	TT	GG	GG	GG	AA
EP012	3.13		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP015	3.13		AA	TT	TT	AA	GG	TT	AA	TT	AA	GG

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP100	3.13		AA	CC	TT	AA	AA	CC	AA	TT	AA	AA
EP039	3.14		AA	TT	TT	AA	GG	TT	AA	GG	AA	GG
EP109	3.14		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP034	3.15		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP119	3.15		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP120	3.15		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP121	3.15		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP166	3.16		GG	CC	TT	AA	AA	CC	AA	TT	AA	AA
EP104	3.17		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP052	3.19		AA	CC	TT	AA	GG	TT	AA	GG	AA	GG
EP112	3.19		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP101	3.2		AA	TT	CC	GG	AA	CC	GG	TT	AA	AA
EP017	3.21		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP057	3.21		AA	TT	TT	AA	GG	TT	GG	TT	AA	AA
EP085	3.21		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP113	3.21		AA	CC	CC	GG	AA	CC	GG	TT	AA	AA
EP158	3.21		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP162	3.22		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP019	3.23		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP167	3.23		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP198	3.23		AA	TT	TT	GG	GG	CC	GG	TT	AA	AA
EP147	3.24		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP168	3.24		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP022	3.25		AA	TT	TT	AA	AA	TT	AA	TT	GG	AA
EP082	3.25		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP160	3.25		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP002	3.26		AA	TT	TT	AA	AA	TT	AA	TT	AA	AA
EP102	3.26		AA	TT	TT	AA	GG	TT	AA	TT	GG	AA
EP156	3.26		AA	TT	TT	AA	GG	CC	GG	TT	GG	AA
EP142	3.27		AA	TT	TT	AA	AA	TT	GG	GG	AA	AA
EP007	3.28		AA	TT	TT	AA	GG	TT	GG	GG	GG	AA
EP020	3.28		AA	TT	TT	AA	GG	TT	AA	TT	GG	AA
EP110	3.28		AA	CC	CC	GG	AA	CC	GG	TT	AA	AA
EP077	3.29		AA	TT	TT	AA	GG	TT	AA	GG	GG	GG
EP153	3.29		AA	TT	TT	AA	GG	TT	AA	GG	GG	AA
EP170	3.29		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP118	3.3		AA	CC	CC	GG	GG	CC	GG	TT	AA	AA
EP125	3.3		AA	TT	CC	GG	AA	CC	GG	TT	GG	GG
EP169	3.3		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP024	3.31		AA	CC	TT	AA	GG	TT	AA	TT	GG	AA
EP140	3.31		AA	TT	CC	AA	GG	TT	GG	GG	AA	AA
EP106	3.32		AA	TT	CC	GG	GG	CC	GG	GG	AA	GG
EP108	3.32		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP115	3.32		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP122	3.32		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP138	3.32		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP150	3.32		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP159	3.32		AA	TT	TT	AA	GG	TT	AA	TT	AA	AA
EP014	3.33		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP117	3.33		AA	TT	CC	GG	GG	CC	GG	TT	AA	GG
EP123	3.33		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP111	3.34		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP126	3.34		AA	CC	CC	GG	AA	CC	GG	TT	GG	GG
EP141	3.34		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP005	3.35		AA	TT	TT	AA	GG	TT	AA	TT	AA	GG
EP013	3.35		AA	TT	TT	AA	GG	TT	AA	GG	AA	AA
EP103	3.35		AA	CC	CC	GG	AA	CC	GG	TT	AA	GG
EP134	3.35		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP151	3.35		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP164	3.35		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP165	3.35		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP008	3.37		AA	TT	TT	GG	GG	TT	GG	TT	AA	AA
EP135	3.37		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP033	3.38		AA	TT	TT	AA	GG	TT	GG	TT	AA	GG
EP139	3.38		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP143	3.38		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA

Accession	GW	QTL-tagging markers	IWB46763	IWB72154	IWB23912	IWB65507	IWB72936	IWB43493	IWB46350	IWB20043	IWB36189	IWB68837
		alleles	A/G	C/T	C/T	A/G	A/G	C/T	A/G	G/T	A/G	A/G
		chrom	2A	2A	2A	3B	4B	5A	5A	6B	7B	7B
		cM	114.7	136.04	208.76	126.23	39.45	72.73	84.77	85.2	66.36	108.1
		-LOG10 P	2.64	3.59	3.01	2.82	2.76	2.84	3.52	2.74	3.06	2.65
		R ² (%)	4.7	6.8	5.5	5.0	4.9	5.1	6.6	4.9	5.6	4.7
		Allelic Effect	0.26	-0.15	-0.32	-0.30	-0.14	-0.19	-0.20	-0.11	-0.15	-0.15
EP171	3.38		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP172	3.38		GG	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP025	3.39		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
EP124	3.39		AA	CC	CC	GG	GG	CC	GG	TT	GG	GG
EP136	3.39		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP146	3.4		AA	TT	TT	AA	GG	TT	GG	TT	GG	AA
EP149	3.4		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP199	3.41		AA	TT	TT	GG	GG	TT	GG	GG	GG	AA
EP137	3.42		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP145	3.42		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP157	3.42		AA	TT	TT	AA	GG	CC	GG	GG	GG	AA
EP174	3.42		AA	CC	CC	GG	GG	CC	GG	TT	AA	GG
EP173	3.43		AA	TT	TT	AA	GG	TT	GG	GG	GG	AA
EP031	3.45		AA	TT	TT	GG	GG	TT	GG	TT	GG	AA
EP152	3.46		AA	TT	TT	AA	GG	TT	GG	GG	AA	AA
EP155	3.49		AA	TT	TT	AA	GG	TT	GG	GG	GG	AA
EP200	3.5		AA	TT	TT	GG	GG	TT	GG	GG	GG	AA
EP029	3.57		AA	CC	TT	AA	GG	TT	GG	TT	GG	AA
SNP allele frequency (-ve effect)			GG	CC	CC	AA	AA	CC	AA	GG	AA	AA
			0.06	0.55	0.16	0.83	0.22	0.26	0.59	0.54	0.71	0.82
SNP allele frequency (+ve effect)			AA	TT	TT	GG	GG	TT	GG	TT	GG	GG
			0.94	0.45	0.84	0.17	0.78	0.74	0.41	0.46	0.29	0.18

Appendix Table 12. Allelic distribution for CIE b* QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by CIE b*.

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP097	11.06		CC	GG	AA	GG	TT	TT	CC	TT
EP192	11.07		CC	GG	AA	GG	TT	TT	CC	TT
EP189	11.11		CC	GG	AA	GG	TT	TT	CC	TT
EP099	11.15		CC	GG	AA	GG	TT	TT	CC	CC
EP194	11.31		CC	GG	AA	GG	TT	TT	CC	TT
EP179	11.41		CC	GG	AA	GG	TT	TT	CC	TT
EP190	11.44		CC	GG	AA	GG	TT	TT	CC	TT
EP098	11.6		CC	GG	AA	GG	TT	TT	CC	CC
EP181	11.65		CC	GG	AA	GG	TT	TT	CC	TT
EP191	11.65		CC	GG	AA	GG	TT	TT	CC	TT
EP188	11.78		CC	GG	AA	GG	TT	TT	CC	TT
EP131	11.93		TT	GG	AA	GG	CC	TT	CC	TT
EP182	12.11		CC	GG	AA	GG	TT	TT	CC	TT
EP195	12.2		CC	GG	AA	GG	TT	TT	CC	TT
EP193	12.33		CC	GG	AA	GG	TT	TT	CC	TT
EP130	12.34		CC	GG	AA	GG	CC	TT	CC	TT
EP184	12.41		CC	GG	AA	GG	TT	TT	CC	TT
EP154	12.43		TT	GG	AA	AA	CC	TT	TT	TT
EP183	12.45		CC	GG	AA	GG	TT	TT	CC	TT
EP127	12.55		TT	GG	AA	GG	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP180	12.57		CC	GG	AA	GG	TT	TT	CC	TT
EP197	12.62		CC	GG	AA	GG	TT	TT	CC	TT
EP133	12.69		TT	GG	AA	GG	TT	TT	CC	TT
EP187	12.74		CC	GG	AA	GG	TT	TT	CC	TT
EP176	12.8		CC	GG	AA	GG	TT	TT	CC	TT
EP186	12.81		CC	GG	AA	GG	TT	TT	CC	TT
EP185	12.99		CC	GG	AA	GG	TT	TT	CC	TT
EP067	13.03		CC	GG	GG	GG	TT	TT	CC	CC
EP175	13.05		CC	GG	AA	GG	TT	TT	CC	TT
EP196	13.25		CC	GG	AA	GG	TT	TT	CC	TT
EP128	13.36		TT	GG	AA	GG	TT	TT	CC	TT
EP063	13.37		CC	GG	GG	GG	TT	TT	CC	CC
EP132	13.52		TT	GG	AA	GG	CC	TT	CC	TT
EP065	13.7		CC	GG	GG	GG	TT	TT	CC	CC
EP048	13.82		TT	GG	AA	GG	CC	TT	CC	TT
EP102	13.83		TT	GG	AA	GG	TT	TT	CC	TT
EP064	13.85		CC	GG	GG	GG	TT	TT	CC	CC
EP095	14.04		TT	GG	AA	GG	TT	TT	CC	CC
EP071	14.13		CC	GG	AA	GG	TT	TT	CC	TT
EP089	14.19		CC	GG	AA	GG	TT	TT	CC	CC
EP093	14.29		CC	GG	AA	GG	TT	TT	CC	TT
EP066	14.4		CC	GG	GG	GG	TT	TT	CC	CC

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP070	14.42		CC	GG	AA	GG	TT	TT	CC	TT
EP091	14.45		CC	GG	AA	GG	TT	TT	CC	CC
EP001	14.54		TT	GG	AA	GG	CC	TT	CC	TT
EP060	14.54		CC	GG	AA	GG	TT	TT	CC	CC
EP092	14.56		CC	GG	AA	GG	TT	TT	CC	CC
EP062	14.6		CC	GG	GG	GG	TT	TT	CC	CC
EP087	14.61		CC	GG	AA	GG	TT	TT	CC	TT
EP028	14.65		CC	GG	AA	GG	CC	TT	CC	TT
EP090	14.71		CC	GG	AA	GG	TT	TT	CC	CC
EP074	14.72		CC	GG	AA	GG	TT	TT	CC	TT
EP163	14.73		CC	GG	AA	GG	TT	TT	CC	TT
EP025	14.74		CC	GG	AA	GG	TT	TT	CC	CC
EP088	14.77		CC	GG	AA	GG	TT	TT	CC	CC
EP142	14.82		TT	GG	AA	GG	TT	TT	CC	TT
EP026	14.88		CC	GG	AA	GG	TT	TT	CC	CC
EP129	15.04		TT	GG	AA	GG	TT	TT	CC	TT
EP011	15.2		CC	GG	AA	GG	TT	TT	CC	TT
EP068	15.22		CC	GG	AA	GG	TT	TT	CC	TT
EP003	15.23		CC	GG	AA	GG	TT	TT	CC	TT
EP021	15.29		TT	GG	AA	AA	TT	TT	TT	TT
EP041	15.31		CC	GG	GG	GG	TT	TT	CC	TT
EP053	15.32		CC	GG	AA	GG	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP080	15.34		CC	GG	AA	GG	TT	TT	CC	TT
EP010	15.35		CC	GG	AA	GG	TT	TT	CC	TT
EP009	15.36		CC	GG	AA	GG	TT	TT	CC	TT
EP036	15.36		CC	GG	AA	GG	TT	TT	CC	TT
EP069	15.36		CC	GG	AA	GG	TT	TT	CC	TT
EP042	15.37		CC	GG	GG	GG	TT	TT	CC	TT
EP057	15.4		CC	GG	AA	GG	TT	TT	CC	TT
EP072	15.42		CC	GG	AA	GG	TT	TT	CC	TT
EP079	15.42		CC	GG	AA	GG	TT	TT	CC	TT
EP078	15.43		CC	GG	AA	GG	TT	TT	CC	TT
EP034	15.44		CC	GG	GG	GG	TT	TT	CC	TT
EP059	15.47		CC	GG	AA	GG	TT	TT	CC	TT
EP061	15.47		CC	GG	AA	GG	TT	TT	CC	TT
EP054	15.61		CC	GG	AA	GG	TT	TT	CC	TT
EP076	15.62		TT	GG	AA	GG	CC	TT	TT	CC
EP044	15.73		CC	GG	AA	GG	TT	TT	CC	TT
EP047	15.79		CC	GG	AA	GG	TT	TT	CC	TT
EP153	15.79		CC	GG	AA	GG	TT	TT	CC	CC
EP198	15.81		CC	GG	AA	GG	TT	TT	CC	TT
EP050	15.84		CC	GG	AA	GG	TT	TT	CC	TT
EP002	15.84		TT	GG	AA	GG	CC	TT	CC	TT
EP004	15.89		TT	GG	AA	AA	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP032	15.89		CC	GG	AA	GG	TT	TT	CC	TT
EP100	15.94		CC	GG	AA	GG	CC	TT	CC	TT
EP052	15.97		CC	GG	AA	GG	TT	TT	CC	TT
EP015	16.03		CC	GG	AA	GG	TT	TT	CC	TT
EP144	16.03		TT	GG	AA	GG	TT	TT	CC	TT
EP084	16.04		CC	GG	AA	AA	TT	TT	CC	TT
EP038	16.14		CC	GG	AA	GG	TT	TT	CC	TT
EP094	16.17		CC	GG	AA	GG	TT	TT	CC	CC
EP033	16.19		CC	GG	AA	GG	TT	TT	CC	TT
EP083	16.23		CC	GG	AA	GG	TT	TT	CC	TT
EP030	16.24		CC	GG	AA	GG	TT	TT	CC	TT
EP046	16.25		CC	GG	AA	GG	TT	TT	CC	TT
EP056	16.28		TT	GG	AA	GG	TT	TT	CC	TT
EP023	16.32		CC	GG	AA	GG	TT	TT	CC	TT
EP039	16.34		CC	GG	AA	GG	TT	TT	CC	TT
EP081	16.34		CC	GG	AA	GG	TT	TT	CC	TT
EP006	16.36		CC	GG	AA	GG	TT	TT	CC	TT
EP019	16.38		CC	GG	AA	GG	TT	TT	CC	TT
EP008	16.45		CC	GG	AA	GG	TT	TT	CC	TT
EP051	16.47		CC	GG	AA	GG	TT	TT	CC	TT
EP085	16.59		CC	GG	AA	GG	TT	TT	CC	TT
EP058	16.66		CC	GG	AA	GG	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP075	16.66		CC	GG	AA	GG	TT	TT	CC	TT
EP049	16.73		CC	GG	AA	GG	TT	TT	CC	CC
EP082	16.76		CC	GG	AA	GG	TT	TT	CC	TT
EP018	16.77		CC	GG	AA	GG	TT	TT	CC	CC
EP024	16.82		TT	GG	AA	GG	TT	TT	CC	TT
EP045	16.86		CC	GG	AA	GG	TT	TT	CC	TT
EP022	16.89		TT	GG	AA	AA	CC	TT	CC	TT
EP166	16.91		CC	GG	AA	GG	CC	TT	CC	TT
EP007	16.96		CC	GG	AA	GG	TT	TT	CC	CC
EP115	17.15		TT	GG	AA	AA	TT	CC	TT	TT
EP199	17.32		CC	GG	AA	AA	TT	TT	CC	CC
EP055	17.38		CC	GG	AA	GG	TT	TT	CC	TT
EP135	17.41		CC	GG	AA	AA	TT	TT	CC	TT
EP200	17.44		CC	GG	AA	AA	TT	TT	CC	CC
EP043	17.52		CC	GG	AA	AA	TT	TT	CC	TT
EP143	17.65		CC	GG	AA	AA	TT	TT	CC	TT
EP157	17.65		CC	GG	AA	GG	TT	TT	CC	TT
EP016	17.68		CC	GG	AA	GG	TT	TT	CC	TT
EP145	17.7		CC	GG	AA	AA	TT	TT	CC	TT
EP156	17.75		CC	GG	AA	GG	TT	TT	CC	CC
EP139	17.81		TT	GG	AA	AA	TT	TT	CC	TT
EP037	17.83		CC	GG	GG	GG	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP110	17.85		TT	AA	AA	AA	CC	CC	TT	CC
EP149	17.86		CC	GG	AA	AA	TT	TT	CC	TT
EP112	17.9		TT	AA	AA	AA	CC	CC	TT	CC
EP126	17.91		CC	AA	AA	AA	CC	CC	TT	CC
EP136	17.91		CC	GG	AA	AA	TT	TT	CC	TT
EP171	17.91		CC	GG	AA	GG	TT	TT	CC	TT
EP086	17.92		CC	GG	AA	AA	TT	TT	CC	TT
EP103	17.92		TT	AA	AA	AA	CC	CC	TT	CC
EP113	17.92		TT	AA	AA	AA	CC	CC	TT	CC
EP160	17.92		CC	GG	AA	GG	TT	TT	CC	TT
EP158	17.99		CC	GG	AA	GG	TT	TT	CC	TT
EP138	18.05		TT	GG	AA	AA	TT	TT	CC	TT
EP159	18.08		CC	GG	AA	AA	TT	TT	CC	TT
EP104	18.09		TT	AA	AA	AA	CC	CC	TT	CC
EP147	18.1		CC	GG	AA	AA	TT	TT	CC	TT
EP137	18.12		CC	GG	AA	AA	TT	TT	CC	TT
EP031	18.15		CC	GG	AA	GG	TT	TT	CC	TT
EP150	18.18		CC	GG	AA	AA	TT	TT	CC	TT
EP168	18.21		CC	GG	AA	GG	TT	TT	CC	TT
EP013	18.31		CC	GG	AA	AA	TT	TT	CC	TT
EP108	18.33		CC	AA	AA	AA	TT	CC	TT	CC
EP134	18.34		TT	GG	AA	AA	TT	TT	CC	TT

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP152	18.35		CC	GG	AA	AA	TT	TT	CC	TT
EP106	18.38		TT	AA	AA	AA	TT	CC	TT	CC
EP077	18.39		CC	GG	AA	GG	TT	TT	CC	CC
EP014	18.4		CC	GG	AA	AA	TT	TT	CC	TT
EP167	18.44		CC	GG	AA	AA	TT	TT	CC	TT
EP096	18.48		CC	GG	AA	AA	TT	TT	CC	TT
EP165	18.53		CC	GG	AA	GG	TT	TT	CC	TT
EP109	18.54		CC	AA	AA	AA	TT	CC	TT	CC
EP029	18.56		CC	GG	AA	GG	TT	TT	CC	CC
EP170	18.58		CC	GG	AA	GG	TT	TT	CC	TT
EP172	18.58		CC	GG	AA	GG	TT	TT	CC	TT
EP169	18.59		CC	GG	AA	GG	TT	TT	CC	TT
EP125	18.67		TT	AA	AA	AA	CC	CC	TT	CC
EP164	18.68		CC	GG	AA	GG	TT	TT	CC	TT
EP123	18.79		TT	AA	AA	AA	CC	CC	TT	CC
EP122	18.88		TT	AA	AA	AA	TT	CC	TT	CC
EP173	18.92		CC	GG	AA	AA	TT	TT	CC	TT
EP114	18.94		TT	AA	AA	AA	TT	CC	TT	CC
EP020	18.99		CC	GG	AA	GG	TT	TT	CC	CC
EP140	19		CC	GG	AA	AA	TT	TT	CC	TT
EP146	19.03		CC	GG	AA	AA	TT	TT	CC	TT
EP105	19.05		TT	AA	AA	AA	TT	CC	TT	CC

Accession	CIE b*	QTL-tagging markers	IWB11958	IWB57773	IWB27216	IWB11992	IWB73411	IWA3196	IWB75144	IWB34768
		alleles	C/T	A/G	A/G	A/G	C/T	C/T	C/T	C/T
		chrom	1B	2A	2B	3A	4B	5A	6A	7B
		cM	115.74	108.99	100.93	141.52	39.47	16.83	75.23	67.34
		-LOG10 P	3.40	2.89	2.79	3.08	3.40	3.10	2.93	3.14
		R ² (%)	6.3	5.2	5.0	5.6	6.3	5.7	5.3	5.8
		Allelic Effect	1.32	3.63	-1.83	1.46	-1.45	4.66	3.35	1.28
EP111	19.05		TT	AA	AA	AA	CC	CC	TT	CC
EP012	19.09		CC	GG	AA	AA	TT	TT	CC	TT
EP017	19.18		CC	GG	AA	AA	TT	TT	CC	TT
EP141	19.21		TT	GG	AA	AA	TT	TT	CC	TT
EP118	19.23		TT	AA	AA	AA	TT	CC	TT	CC
EP162	19.24		CC	GG	AA	AA	TT	TT	CC	TT
EP107	19.32		TT	AA	AA	AA	TT	CC	TT	CC
EP116	19.36		TT	AA	AA	AA	CC	CC	TT	CC
EP117	19.37		TT	AA	AA	AA	TT	CC	TT	CC
EP155	19.45		CC	GG	AA	AA	TT	TT	CC	CC
EP124	19.65		CC	AA	AA	AA	TT	CC	TT	CC
EP101	19.68		TT	AA	AA	AA	TT	CC	TT	CC
EP120	20.1		TT	AA	AA	AA	TT	CC	TT	CC
EP151	20.13		CC	GG	AA	AA	TT	TT	CC	TT
EP174	20.27		TT	AA	AA	AA	TT	CC	TT	CC
EP005	20.29		CC	GG	AA	GG	TT	TT	CC	TT
EP119	20.67		CC	AA	AA	AA	TT	CC	CC	CC
EP121	20.89		CC	AA	GG	AA	TT	CC	CC	CC
SNP allele frequency (-ve effect)			TT	GG	AA	GG	CC	TT	TT	TT
			0.23	0.87	0.06	0.68	0.11	0.86	0.14	0.71
SNP allele frequency (+ve effect)			CC	AA	GG	AA	TT	CC	CC	CC
			0.77	0.13	0.94	0.32	0.89	0.14	0.86	0.29

Appendix Table 13. Allelic distribution for CIE L* QTL-tagging SNPs in the Ethiopian durum wheat panel. Accessions are listed by CIE L*.

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP097	43.53		TT	CC	CC	GG	AA	AA	GG	CC
EP194	44.23		TT	TT	CC	GG	AA	AA	GG	CC
EP181	44.28		TT	TT	CC	GG	AA	AA	GG	CC
EP192	44.58		TT	TT	CC	GG	AA	AA	GG	CC
EP176	44.72		TT	TT	CC	GG	AA	AA	GG	CC
EP191	44.74		TT	TT	CC	GG	AA	AA	GG	CC
EP026	44.77		CC	CC	CC	GG	GG	AA	GG	TT
EP175	45.29		TT	TT	CC	GG	AA	AA	GG	CC
EP154	45.33		TT	CC	CC	GG	AA	AA	TT	TT
EP099	45.57		TT	TT	CC	GG	GG	AA	GG	CC
EP071	45.76		CC	TT	CC	GG	AA	GG	GG	CC
EP028	45.85		TT	CC	TT	GG	AA	AA	TT	CC
EP098	45.94		TT	TT	CC	GG	GG	AA	GG	CC
EP182	46.15		TT	TT	CC	GG	AA	AA	GG	CC
EP070	46.23		CC	TT	CC	GG	AA	GG	GG	CC
EP065	46.29		TT	TT	CC	GG	GG	AA	GG	CC
EP062	46.34		TT	TT	CC	GG	GG	AA	GG	CC
EP011	46.44		CC	TT	CC	GG	AA	GG	GG	CC
EP193	46.51		TT	TT	CC	GG	AA	AA	GG	CC
EP183	46.57		TT	TT	CC	GG	AA	AA	GG	CC

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP189	46.57		TT	TT	CC	GG	AA	AA	GG	CC
EP179	46.68		TT	TT	CC	GG	AA	AA	GG	CC
EP197	46.73		TT	TT	CC	GG	AA	AA	GG	CC
EP188	46.75		TT	TT	CC	GG	AA	AA	GG	CC
EP187	46.87		TT	TT	CC	GG	AA	AA	GG	CC
EP064	46.93		TT	TT	CC	GG	GG	AA	GG	CC
EP067	46.93		TT	TT	CC	GG	GG	AA	GG	CC
EP185	46.94		TT	TT	CC	GG	AA	AA	GG	CC
EP063	47.08		TT	TT	CC	GG	GG	AA	GG	CC
EP127	47.1		TT	TT	CC	GG	GG	AA	GG	CC
EP038	47.13		CC	TT	CC	GG	AA	AA	GG	CC
EP195	47.21		TT	TT	CC	GG	AA	AA	GG	CC
EP091	47.34		TT	TT	CC	GG	GG	GG	GG	CC
EP196	47.37		TT	TT	CC	GG	AA	AA	GG	CC
EP066	47.39		TT	TT	CC	GG	GG	AA	GG	CC
EP010	47.4		CC	TT	CC	GG	AA	GG	GG	CC
EP128	47.49		TT	TT	CC	GG	GG	AA	GG	CC
EP069	47.51		CC	TT	CC	GG	AA	GG	GG	CC
EP090	47.57		TT	TT	CC	GG	GG	GG	GG	CC
EP186	47.65		TT	TT	CC	GG	AA	AA	GG	CC
EP130	47.76		CC	CC	CC	GG	GG	AA	GG	CC
EP131	47.79		TT	CC	CC	GG	GG	AA	GG	CC

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP184	47.88		TT	TT	CC	GG	AA	AA	GG	CC
EP180	48.13		TT	TT	CC	GG	AA	AA	GG	CC
EP133	48.21		TT	TT	CC	GG	GG	AA	GG	CC
EP072	48.22		CC	TT	CC	GG	AA	GG	GG	CC
EP190	48.32		TT	TT	CC	GG	AA	AA	GG	CC
EP089	48.44		TT	TT	CC	GG	GG	GG	GG	CC
EP068	48.59		CC	TT	CC	GG	AA	GG	GG	CC
EP092	48.82		TT	TT	CC	GG	GG	GG	GG	CC
EP081	49.27		CC	TT	CC	GG	AA	AA	GG	CC
EP088	49.37		TT	TT	CC	GG	AA	GG	GG	CC
EP061	50.03		CC	TT	TT	GG	AA	AA	GG	CC
EP080	50.26		CC	TT	CC	GG	AA	AA	GG	CC
EP093	50.28		CC	TT	CC	GG	GG	GG	GG	CC
EP037	50.3		CC	TT	TT	GG	AA	AA	GG	CC
EP003	50.36		CC	TT	CC	GG	AA	AA	GG	CC
EP048	50.4		TT	CC	CC	GG	GG	AA	GG	CC
EP079	50.58		CC	TT	CC	GG	AA	AA	GG	CC
EP074	50.8		CC	TT	CC	GG	AA	AA	GG	CC
EP006	50.9		CC	TT	CC	AA	GG	GG	GG	CC
EP055	51.37		CC	TT	CC	GG	AA	AA	GG	CC
EP078	51.56		CC	TT	CC	AA	GG	AA	GG	CC
EP051	52.51		CC	TT	CC	GG	AA	AA	GG	CC

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP087	52.67	CC	TT	CC	GG	AA	GG	GG	CC	
EP132	52.89	TT	TT	CC	GG	GG	AA	GG	CC	
EP050	53.67	CC	TT	CC	GG	AA	AA	GG	CC	
EP129	54.23	CC	TT	CC	GG	GG	AA	GG	CC	
EP054	54.7	CC	TT	CC	GG	AA	AA	GG	CC	
EP053	54.74	CC	TT	TT	GG	AA	AA	GG	CC	
EP018	55.91	CC	TT	CC	AA	GG	AA	GG	CC	
EP004	58.3	CC	TT	CC	GG	GG	AA	GG	CC	
EP021	58.42	CC	TT	TT	GG	AA	AA	GG	CC	
EP117	58.52	TT	TT	TT	GG	AA	GG	TT	CC	
EP153	58.59	CC	TT	TT	GG	GG	AA	GG	CC	
EP009	58.82	CC	TT	TT	AA	AA	AA	GG	CC	
EP101	59	TT	CC	TT	AA	AA	GG	TT	CC	
EP056	59.02	CC	TT	TT	AA	AA	AA	GG	CC	
EP174	59.15	TT	CC	CC	GG	AA	GG	TT	CC	
EP076	59.25	TT	TT	CC	AA	AA	AA	GG	CC	
EP118	59.32	TT	CC	CC	AA	AA	AA	TT	CC	
EP032	59.43	CC	TT	TT	GG	AA	AA	GG	CC	
EP044	59.6	CC	TT	TT	GG	GG	AA	GG	CC	
EP057	59.62	CC	TT	TT	GG	AA	AA	GG	CC	
EP114	59.77	TT	CC	CC	AA	AA	AA	TT	CC	
EP112	59.9	TT	CC	CC	GG	AA	AA	TT	CC	

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP144	60.02		CC	TT	CC	GG	GG	AA	GG	CC
EP125	60.16		TT	CC	TT	GG	AA	AA	TT	CC
EP116	60.18		TT	CC	CC	AA	AA	AA	TT	CC
EP107	60.19		TT	TT	CC	AA	AA	AA	TT	CC
EP113	60.24		TT	CC	CC	GG	AA	AA	TT	TT
EP047	60.36		TT	TT	TT	GG	GG	AA	GG	CC
EP123	60.48		TT	CC	CC	GG	AA	AA	TT	CC
EP124	60.51		TT	CC	CC	AA	AA	AA	TT	TT
EP033	60.52		CC	TT	TT	AA	AA	AA	GG	CC
EP122	60.75		TT	CC	CC	AA	AA	AA	GG	TT
EP034	60.76		CC	TT	TT	GG	AA	AA	GG	CC
EP046	60.76		TT	TT	TT	GG	GG	AA	GG	CC
EP120	60.78		TT	CC	CC	GG	AA	AA	TT	CC
EP104	60.81		TT	CC	CC	GG	AA	AA	TT	CC
EP041	60.83		CC	TT	TT	GG	AA	AA	GG	CC
EP045	60.85		CC	TT	TT	GG	AA	AA	GG	CC
EP052	60.85		CC	TT	CC	GG	AA	AA	GG	CC
EP084	60.91		CC	TT	TT	AA	AA	AA	GG	CC
EP075	60.94		CC	TT	TT	GG	AA	AA	GG	CC
EP163	61.04		CC	TT	TT	GG	GG	AA	GG	CC
EP083	61.05		CC	TT	TT	GG	AA	AA	GG	CC
EP042	61.07		CC	TT	TT	GG	AA	AA	GG	CC

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP036	61.2		CC	TT	CC	GG	AA	AA	GG	CC
EP059	61.26		CC	TT	TT	GG	AA	AA	GG	CC
EP119	61.41		TT	TT	CC	AA	AA	AA	GG	CC
EP039	61.42		CC	TT	TT	GG	GG	AA	GG	CC
EP029	61.5		CC	CC	CC	GG	GG	AA	GG	CC
EP030	61.53		CC	TT	TT	GG	GG	AA	GG	CC
EP100	61.55		CC	TT	CC	GG	AA	AA	GG	CC
EP014	61.58		CC	TT	TT	GG	AA	AA	GG	CC
EP008	61.6		CC	TT	TT	GG	GG	AA	GG	CC
EP025	61.62		CC	CC	CC	GG	GG	AA	GG	TT
EP166	61.63		CC	CC	CC	GG	AA	AA	GG	CC
EP108	61.68		TT	CC	CC	AA	AA	AA	TT	CC
EP007	61.73		TT	TT	TT	GG	GG	AA	GG	CC
EP015	61.87		CC	TT	TT	GG	AA	AA	GG	CC
EP023	61.87		CC	TT	CC	GG	GG	AA	GG	CC
EP106	61.9		TT	CC	TT	GG	GG	GG	TT	CC
EP077	61.93		TT	TT	TT	GG	GG	AA	GG	CC
EP016	61.94		CC	TT	TT	AA	AA	AA	GG	CC
EP082	61.98		CC	TT	TT	GG	AA	AA	GG	CC
EP115	62.11		TT	CC	CC	AA	AA	AA	TT	TT
EP162	62.17		CC	TT	TT	AA	AA	AA	GG	CC
EP049	62.19		CC	TT	TT	AA	AA	AA	GG	CC

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP167	62.19	CC	TT	TT	AA	AA	AA	GG	CC	
EP024	62.21	TT	TT	CC	GG	GG	AA	GG	CC	
EP121	62.31	TT	CC	CC	AA	AA	AA	GG	CC	
EP031	62.32	CC	TT	TT	GG	GG	AA	GG	CC	
EP058	62.32	TT	TT	TT	GG	GG	AA	GG	CC	
EP111	62.35	TT	CC	CC	AA	AA	AA	TT	CC	
EP019	62.44	CC	TT	TT	AA	AA	AA	GG	CC	
EP142	62.87	CC	CC	TT	GG	GG	AA	GG	CC	
EP085	62.92	CC	TT	TT	GG	AA	AA	GG	CC	
EP126	62.97	TT	CC	CC	GG	AA	AA	TT	TT	
EP020	63	CC	TT	TT	GG	AA	AA	GG	CC	
EP159	63.05	CC	TT	TT	AA	AA	AA	GG	CC	
EP002	63.13	CC	TT	TT	GG	GG	AA	GG	CC	
EP157	63.28	CC	TT	TT	GG	GG	AA	GG	CC	
EP095	63.34	CC	TT	TT	GG	AA	AA	GG	CC	
EP005	63.4	CC	TT	TT	GG	AA	AA	GG	CC	
EP060	63.44	CC	TT	CC	GG	AA	AA	GG	CC	
EP094	63.45	CC	TT	TT	AA	AA	AA	GG	CC	
EP096	63.47	CC	TT	TT	GG	AA	AA	GG	CC	
EP110	63.48	TT	CC	CC	GG	GG	AA	GG	TT	
EP102	63.63	CC	TT	TT	GG	GG	AA	GG	CC	
EP012	63.67	CC	TT	TT	AA	AA	AA	GG	CC	

Accession	CIE L*	QTL-tagging markers	IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
		alleles	C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
		chrom	1A	2A	2A	5A	6A	7A	7A	7B
		cM	87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
		-LOG10 P	3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
		R ² (%)	6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
		Allelic Effect	5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP134	63.76		CC	TT	CC	GG	GG	AA	GG	CC
EP043	63.79		CC	TT	TT	GG	AA	AA	GG	CC
EP156	63.79		CC	TT	TT	GG	GG	AA	GG	CC
EP173	63.96		CC	TT	TT	GG	GG	AA	GG	CC
EP103	64.02		TT	CC	CC	GG	AA	AA	TT	CC
EP017	64.03		CC	TT	TT	AA	AA	AA	GG	CC
EP164	64.09		CC	TT	TT	GG	GG	AA	GG	CC
EP013	64.16		CC	TT	TT	AA	AA	AA	GG	CC
EP172	64.21		CC	TT	TT	GG	GG	AA	GG	CC
EP139	64.22		CC	TT	CC	GG	GG	AA	GG	CC
EP171	64.22		CC	TT	TT	GG	GG	AA	GG	CC
EP141	64.28		CC	TT	CC	GG	GG	AA	GG	CC
EP198	64.29		CC	TT	TT	GG	GG	AA	GG	CC
EP168	64.35		CC	TT	TT	GG	GG	AA	GG	CC
EP138	64.37		CC	TT	CC	GG	GG	AA	GG	CC
EP169	64.4		CC	TT	TT	GG	GG	AA	GG	CC
EP160	64.43		CC	TT	TT	GG	GG	AA	GG	CC
EP001	64.5		CC	TT	TT	GG	GG	AA	GG	CC
EP155	64.54		CC	TT	TT	GG	GG	AA	GG	CC
EP165	64.57		CC	TT	TT	GG	GG	AA	GG	CC
EP151	64.78		CC	CC	TT	GG	GG	AA	GG	CC
EP170	64.81		CC	TT	TT	GG	GG	AA	GG	CC

Accession CIE L*		QTL-tagging markers							
		IWB65551	IWB82861	IWB72154	IWB7271	IWB70454	IWB66972	IWB72494	IWB62029
alleles		C/T	C/T	C/T	A/G	A/G	A/G	G/T	C/T
chrom		1A	2A	2A	5A	6A	7A	7A	7B
cM		87	117.05	136.04	84.72	117.1	113.61	143.19	165.05
-LOG10 P		3.17	3.30	5.23	2.67	2.65	2.76	3.14	3.26
R ² (%)		6.0	6.3	11.0	4.9	4.8	5.1	5.9	6.2
Allelic Effect		5.19	-5.35	-4.96	1.62	-4.59	5.85	7.48	6.66
EP109	64.93	TT	CC	CC	AA	AA	AA	TT	TT
EP146	65.02	CC	TT	TT	GG	GG	AA	GG	CC
EP086	65.2	CC	TT	TT	AA	AA	AA	GG	CC
EP158	65.36	CC	TT	TT	GG	GG	AA	GG	CC
EP022	65.52	CC	TT	TT	AA	AA	AA	GG	CC
EP140	66.04	CC	TT	TT	GG	GG	AA	GG	CC
EP199	66.25	CC	TT	TT	GG	GG	AA	GG	CC
EP200	66.54	CC	TT	TT	GG	GG	AA	GG	CC
EP152	66.62	CC	CC	TT	GG	GG	AA	GG	CC
EP149	66.89	CC	CC	TT	GG	GG	AA	GG	CC
EP135	66.92	CC	CC	TT	GG	GG	AA	GG	CC
EP145	66.93	CC	CC	TT	GG	GG	AA	GG	CC
EP143	67.03	CC	CC	TT	GG	GG	AA	GG	CC
EP136	67.07	CC	CC	TT	GG	GG	AA	GG	CC
EP147	67.25	CC	CC	TT	GG	GG	AA	GG	CC
EP137	67.28	CC	CC	TT	GG	GG	AA	GG	CC
EP105	67.43	CC	CC	TT	AA	AA	AA	TT	CC
EP150	67.78	CC	CC	TT	GG	GG	AA	GG	CC
SNP allele frequency (-ve effect)		TT	CC	CC	GG	AA	GG	TT	TT
		0.40	0.23	0.55	0.83	0.58	0.10	0.13	0.05
SNP allele frequency (+ve effect)		CC	TT	TT	AA	GG	AA	GG	CC
		0.60	0.77	0.45	0.17	0.42	0.90	0.88	0.95

Appendix Table 14. Allelic distribution for CIE a* QTL-tagging SNPs in the Ethiopian durum wheat panel.

Accessions are listed by CIE a*.

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP200	6.53		AA	TT	TT	TT	AA
EP199	6.64		AA	TT	TT	TT	AA
EP135	7.04		GG	CC	TT	TT	AA
EP147	7.06		GG	CC	TT	TT	AA
EP143	7.16		GG	CC	TT	TT	AA
EP150	7.16		GG	CC	TT	TT	AA
EP103	7.17		AA	CC	CC	CC	AA
EP137	7.2		GG	CC	TT	TT	AA
EP106	7.23		GG	CC	TT	CC	GG
EP115	7.23		GG	CC	CC	CC	AA
EP136	7.24		GG	CC	TT	TT	AA
EP110	7.27		AA	CC	CC	CC	AA
EP145	7.38		GG	CC	TT	TT	AA
EP126	7.4		AA	CC	CC	CC	AA
EP149	7.41		GG	CC	TT	TT	AA
EP109	7.43		AA	CC	CC	CC	AA
EP001	7.45		GG	TT	TT	TT	AA
EP152	7.46		GG	CC	TT	TT	AA
EP022	7.49		GG	TT	TT	TT	AA
EP140	7.49		GG	TT	TT	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP158	7.5		AA	TT	TT	TT	AA
EP157	7.54		AA	TT	TT	TT	AA
EP119	7.57		GG	TT	CC	CC	AA
EP160	7.57		AA	TT	TT	TT	AA
EP043	7.61		AA	TT	TT	TT	AA
EP125	7.61		AA	CC	TT	CC	AA
EP104	7.62		AA	CC	CC	CC	AA
EP086	7.63		GG	TT	TT	TT	AA
EP123	7.65		AA	CC	CC	CC	AA
EP156	7.66		GG	TT	TT	TT	AA
EP012	7.67		AA	TT	TT	TT	AA
EP112	7.67		AA	CC	CC	CC	AA
EP017	7.7		GG	TT	TT	TT	AA
EP155	7.72		GG	TT	TT	TT	AA
EP120	7.73		GG	CC	CC	CC	AA
EP095	7.74		AA	TT	TT	TT	AA
EP159	7.76		GG	TT	TT	TT	AA
EP020	7.78		AA	TT	TT	TT	AA
EP146	7.78		GG	TT	TT	TT	AA
EP111	7.8		AA	CC	CC	CC	AA
EP121	7.81		GG	CC	CC	CC	AA
EP122	7.82		GG	CC	CC	CC	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP170	7.82		AA	TT	TT	TT	AA
EP107	7.83		AA	TT	CC	CC	AA
EP013	7.85		GG	TT	TT	TT	AA
EP102	7.86		GG	TT	TT	TT	AA
EP124	7.87		AA	CC	CC	CC	AA
EP165	7.88		AA	TT	TT	TT	AA
EP138	7.89		GG	TT	CC	TT	AA
EP169	7.91		AA	TT	TT	TT	AA
EP134	7.92		GG	TT	CC	TT	AA
EP025	7.93		GG	CC	CC	TT	AA
EP173	7.93		GG	TT	TT	TT	AA
EP171	7.95		AA	TT	TT	TT	AA
EP139	7.97		GG	TT	CC	TT	AA
EP118	7.98		GG	CC	CC	CC	AA
EP005	8.01		AA	TT	TT	TT	AA
EP029	8.03		GG	CC	CC	TT	AA
EP141	8.04		GG	TT	CC	TT	AA
EP168	8.07		AA	TT	TT	TT	AA
EP077	8.09		AA	TT	TT	TT	AA
EP113	8.09		AA	CC	CC	CC	AA
EP167	8.1		GG	TT	TT	TT	AA
EP108	8.11		GG	CC	CC	CC	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP162	8.12		GG	TT	TT	TT	AA
EP031	8.13		GG	TT	TT	TT	AA
EP164	8.13		AA	TT	TT	TT	AA
EP151	8.14		GG	CC	TT	TT	AA
EP172	8.14		AA	TT	TT	TT	AA
EP060	8.15		AA	TT	CC	TT	AA
EP142	8.16		GG	CC	TT	TT	AA
EP096	8.17		GG	TT	TT	TT	AA
EP116	8.29		GG	CC	CC	CC	AA
EP114	8.31		GG	CC	CC	CC	AA
EP174	8.31		GG	CC	CC	CC	GG
EP163	8.32		GG	TT	TT	TT	AA
EP014	8.33		GG	TT	TT	TT	AA
EP117	8.34		GG	CC	TT	CC	GG
EP094	8.35		AA	TT	TT	TT	AA
EP101	8.35		GG	CC	TT	CC	GG
EP105	8.35		AA	CC	CC	CC	AA
EP036	8.4		AA	TT	CC	TT	AA
EP034	8.41		AA	TT	TT	TT	AA
EP007	8.46		GG	TT	TT	TT	AA
EP019	8.48		GG	TT	TT	TT	AA
EP002	8.49		GG	TT	TT	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP059	8.5		GG	TT	TT	TT	AA
EP042	8.52		AA	TT	TT	TT	AA
EP030	8.54		GG	TT	TT	TT	AA
EP198	8.54		AA	TT	TT	TT	AA
EP085	8.59		GG	TT	TT	TT	AA
EP024	8.62		GG	TT	CC	TT	AA
EP008	8.63		AA	TT	TT	TT	AA
EP015	8.63		GG	TT	TT	TT	AA
EP004	8.66		GG	TT	CC	TT	AA
EP041	8.66		AA	TT	TT	TT	AA
EP082	8.66		GG	TT	TT	TT	AA
EP044	8.73		AA	TT	TT	TT	AA
EP058	8.76		GG	TT	TT	TT	AA
EP052	8.78		AA	TT	CC	TT	AA
EP023	8.79		AA	TT	CC	TT	AA
EP033	8.8		GG	TT	TT	TT	AA
EP049	8.8		GG	TT	TT	TT	AA
EP166	8.81		GG	CC	CC	TT	AA
EP039	8.85		AA	TT	TT	TT	AA
EP016	8.86		GG	TT	TT	TT	AA
EP100	8.87		GG	TT	CC	TT	AA
EP047	8.88		GG	TT	TT	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP075	8.93		GG	TT	TT	TT	AA
EP083	8.95		AA	TT	TT	TT	AA
EP057	8.96		GG	TT	TT	TT	AA
EP032	8.98		GG	TT	TT	TT	AA
EP046	9.04		GG	TT	TT	TT	AA
EP084	9.04		GG	TT	TT	TT	AA
EP144	9.14		GG	TT	CC	TT	AA
EP009	9.18		GG	TT	TT	TT	AA
EP045	9.18		GG	TT	TT	TT	AA
EP153	9.19		GG	TT	TT	TT	AA
EP056	9.2		AA	TT	TT	TT	AA
EP076	9.41		GG	TT	CC	TT	AA
EP021	9.55		GG	TT	TT	TT	AA
EP018	10.06		GG	TT	CC	TT	AA
EP054	10.06		GG	TT	CC	TT	AA
EP132	10.2		GG	TT	CC	TT	AA
EP053	10.22		GG	TT	TT	TT	AA
EP129	10.24		GG	TT	CC	TT	AA
EP050	10.97		AA	TT	CC	TT	AA
EP048	11.01		GG	CC	CC	TT	AA
EP087	11.12		GG	TT	CC	TT	GG
EP003	11.19		AA	TT	CC	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP093	11.32		AA	TT	CC	TT	GG
EP078	11.42		AA	TT	CC	TT	AA
EP051	11.51		AA	TT	CC	TT	AA
EP063	11.56		AA	TT	CC	TT	AA
EP088	11.57		GG	TT	CC	TT	GG
EP074	11.59		GG	TT	CC	TT	AA
EP092	11.6		AA	TT	CC	TT	GG
EP006	11.61		GG	TT	CC	TT	GG
EP067	11.61		AA	TT	CC	TT	AA
EP127	11.69		GG	TT	CC	TT	AA
EP131	11.73		GG	CC	CC	TT	AA
EP066	11.74		AA	TT	CC	TT	AA
EP080	11.75		GG	TT	CC	TT	AA
EP079	11.76		GG	TT	CC	TT	AA
EP055	11.79		GG	TT	CC	TT	AA
EP133	11.81		GG	TT	CC	TT	AA
EP175	11.83		GG	TT	CC	TT	AA
EP089	11.87		AA	TT	CC	TT	GG
EP010	11.97		GG	TT	CC	TT	GG
EP065	11.97		AA	TT	CC	TT	AA
EP128	11.98		GG	TT	CC	TT	AA
EP061	12		GG	TT	TT	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP068	12		GG	TT	CC	TT	GG
EP176	12.06		GG	TT	CC	TT	AA
EP196	12.06		GG	TT	CC	TT	AA
EP130	12.15		GG	CC	CC	TT	AA
EP028	12.19		GG	CC	TT	TT	AA
EP099	12.19		AA	TT	CC	TT	AA
EP081	12.2		GG	TT	CC	TT	AA
EP062	12.22		AA	TT	CC	TT	AA
EP064	12.22		AA	TT	CC	TT	AA
EP098	12.23		AA	TT	CC	TT	AA
EP072	12.24		GG	TT	CC	TT	GG
EP090	12.3		AA	TT	CC	TT	GG
EP180	12.33		GG	TT	CC	TT	AA
EP188	12.37		GG	TT	CC	TT	AA
EP185	12.4		GG	TT	CC	TT	AA
EP091	12.42		AA	TT	CC	TT	GG
EP197	12.42		GG	TT	CC	TT	AA
EP069	12.44		GG	TT	CC	TT	GG
EP189	12.44		GG	TT	CC	TT	AA
EP154	12.46		GG	CC	CC	TT	AA
EP190	12.46		GG	TT	CC	TT	AA
EP193	12.48		GG	TT	CC	TT	AA

Accession	CIE a*	QTL-tagging markers	IWB57868	IWB8286	IWB72154	IWA3196	IWB66972
		alleles	A/G	C/T	C/T	C/T	A/G
		chrom	1A	2A	2A	5A	7A
		cM	1.74	117.05	136.04	16.83	113.61
		-LOG10 P	2.53	2.98	5.39	2.81	2.81
		R ² (%)	4.6	5.6	11.4	5.2	5.2
		Allelic Effect	-0.83	1.38	1.36	-4.07	-1.58
EP026	12.49		GG	CC	CC	TT	AA
EP037	12.5		AA	TT	TT	TT	AA
EP038	12.57		AA	TT	CC	TT	AA
EP179	12.57		GG	TT	CC	TT	AA
EP184	12.58		GG	TT	CC	TT	AA
EP186	12.63		GG	TT	CC	TT	AA
EP071	12.74		GG	TT	CC	TT	GG
EP187	12.76		GG	TT	CC	TT	AA
EP070	12.77		GG	TT	CC	TT	GG
EP183	12.77		GG	TT	CC	TT	AA
EP011	12.84		GG	TT	CC	TT	GG
EP195	12.88		GG	TT	CC	TT	AA
EP192	12.98		GG	TT	CC	TT	AA
EP097	13.06		AA	TT	CC	TT	AA
EP191	13.09		GG	TT	CC	TT	AA
EP194	13.11		GG	TT	CC	TT	AA
EP181	13.18		GG	TT	CC	TT	AA
EP182	13.2		GG	TT	CC	TT	AA
SNP allele frequency (-ve effect)			AA	TT	TT	CC	AA
			0.34	0.77	0.45	0.14	0.90
SNP allele frequency (+ve effect)			GG	CC	CC	TT	GG
			0.66	0.23	0.55	0.86	0.10