

**Genetic Diversity, Genotype-by-Environment Interaction and Genome Wide
Association of Stripe Rust (*Puccinia striiformis* f.sp. tritici) in Bread Wheat (*Triticum
aestivum* L.) Genotypes**



Genet Atsbeha Fiseha

A Dissertation Submitted to
Department of Applied Biology,
School of Applied Natural Science

Presented in Partial Fulfillment of the Requirement for the Degree of Doctor of Philosophy
in Biotechnology (Specialization in Plant Biotechnology)

Office of Graduate Studies
Adama Science and Technology University

March, 2024
Adama, Ethiopia

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DECLARATION

I hereby declare that this Dissertation entitled “Genetic Diversity, Genotype-by-Environment Interaction and Genome Wide Association of Stripe Rust (*Puccinia striiformis* f.sp. tritici) in Bread Wheat (*Triticum aestivum* L.) Genotypes” is my original work. This work has not been submitted for an award of any academic degree, diploma or certificate in any other university. All sources of materials used for this thesis have been duly acknowledged through appropriate citations.

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Signature

Date

RECOMMENDATION

I/we, the supervisor(s) of this dissertation, hereby certify that I/we have read and revised the dissertation entitled “Genetic Diversity, Genotype-by-Environment Interaction and Genome Wide Association of Stripe Rust (*Puccinia striiformis* f.sp. tritici) in Bread Wheat (*Triticum aestivum* L.) Genotypes” prepared under my/our guidance by Genet Atsbeha Fiseha submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Biotechnology. Therefore, I/we recommend the submission of the dissertation to the department for further review and defence.

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I/we hereby certify that the recommendations and suggestions made by the board of examiners are appropriately incorporated into the final version of the dissertation entitled “Genetic Diversity, Genotype-by-Environment Interaction and Genome Wide Association of Stripe Rust (*Puccinia striiformis* f.sp. tritici) in Bread Wheat (*Triticum aestivum* L.) Genotypes” by Genet Atsbeha.

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PUBLICATIONS DURING CANDIDATURE

- Genet Atsbeha, Kassahun Tesfaye, Tilahun Mekonnen, Teklehaimanot Haileselassie and Mulugeta Kebede (2023). Genetic diversity and population structure analysis of bread wheat (*Triticum aestivum* L.) germplasms as revealed by inter simple sequence repeat (ISSR) markers. Springer Nature B.V. 2023, Genetic Resource and Crop Evolution, <https://doi.org/10.1007/s10722-023-01791-6>
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LIST OF ACRONYMS AND ABBREVIATIONS

ADT	Adaptation Trial
AMMI	Additive Main Effects and Multiplicative Interactions
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
BIC	Bayesian Information Criterion
BLINK	Bayesian-Information and Linkage-Disequilibrium Iteratively Nested Keyway
CI	Coefficient of Infection
CIMMYT	International Maize and Wheat Improvement Center
CMLM	Compressed Mixed Linear Lode
CTAB	Cetyltrimethylammonium Bromide
DArT	Diversity Array Technology
DS	Disease Severity
ECMLM	Enriched Compressed Mixed Linear Model
FarmCPU	Fixed and Random Model Circulating Probability Unification
f. sp.	Forma Specialis
FR	Field Response
GAPIT	Genome Association and Prediction Integrated Tools
GBS	Genotyping-by-Sequencing
GEI	Genotype Environment Interaction
GEE	Genotype Environment Interaction
GLM	General Linear Model
GWAS	Genome-wide Association Study
GxE	Genotype-by-Environment Interaction
HR	Hypersensitive Response
HRWSN	High-Rain Wheat Screening Nursery
HRWYT	High Rain Wheat Yield Trial
IBWSN	International Bread Wheat Screening Nursery
ISEPON	International Septoria Observation Nursery
ISSR	Inter Simple Sequence Repeat
IWGSC	International Wheat Genome Sequencing Consortium

LD	Linkage Disequilibrium
MAPK	Mitogen-Activated Protein Kinase
MAS	Marker Assisted Selection
MLM	Mixed Liner Model
PCA	Principal Component Analysis
MTA	Marker Trait Association
PVT	Preliminary Variety Trial
Q-Q	Quantile-Quantile
QTL	Quantitative Trait Locus
RAPD	Randomly Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
SNP	Single Nucleotide Polymorphism
SR	Seedling Response
SSRs	Simple Sequence Repeats
SUPER	Settlement of Mixed Linear Model Under Progressively Exclusive Relationship
TASSEL	Trait Analysis by Association, Evolution and Linkage
WGS	Whole Genome Sequence
Yr	Yellow Rust Resistant Gene

ABSTRACT

Wheat is Ethiopia's staple crop, accounting for 15% of daily calorie intake. However, due to population growth, changing food preferences, a strong urbanization trend, climate change, increased input costs, limited access to advanced production technologies, and increased intensity of abiotic and biotic stresses, which make the wheat demand-supply chain, is extremely volatile and can cause social instabilities. Fungal diseases, such as stripe rust, are severe bottlenecks in Ethiopian wheat production. Stripe rust caused by *Puccinia striiformis* f. sp. *tritici*, is a severe disease of wheat worldwide, including Ethiopia, causing up to 100% wheat yield loss in the worst season. The use of resistant cultivars is considered to be the most effective and durable management technique for controlling the disease. Accordingly, this study was aimed to explore genetic diversity, heritability, genotype-by-environment interaction (G×E) and genomic regions associated with stripe rust (*Puccinia striiformis* f.sp. *tritici*) resistance traits in bread wheat genotypes. Besides, genetic diversity and population structure of 180 bread wheat genotypes representing eight populations were analyzed using ten polymorphic inter simple sequence repeat (ISSR) markers. High within-populations genetic diversity with a mean allele values of 1.47, effective alleles of 1.33, Shannon's information index of 0.29, Nei's gene diversity of 0.19, and percent polymorphic loci (PPL) of 80.5% were obtained. Analysis of molecular variance (AMOVA) revealed that 95% of the total genetic variation resides within populations, while the remaining 5% was accounted to among populations. Moreover, the extent of genetic variability, heritability and genotype-environment interaction in the 180 bread wheat genotypes were investigated using field-based phenotyping of 12 agro-morphological traits. This experiment was positioned at alpha lattice design in two replications in Ethiopia at Kulumsa Agricultural Research Center (KARC), Meraro (substation of KARC) and Holeta Agricultural Research Center (HARC). Moderate heritability and genetic advance were observed in plant height (50%, 5.5%), spike length (38%, 5.3%), number of kernels per spike (50%, 5.23%), and thousand kernel weights (41%, 4.38%), respectively. Moreover, combined analysis of variance and AMMI analysis showed highly significant differences for environment and genotype, in which grain yields were significantly affected by environment, accounting for 55.22% of the total variation. However, genotype and genotype-environment interaction (G×E) accounted for 27.46% and 17.44%, respectively. Moreover an investigation on virulence variability of four *P. striiformis* isolates from Ethiopia, efficiency of known *Yr* resistance genes and wheat cultivars against the isolates revealed presence of host-pathogen interaction. For instance in isolate 2, based on coefficient of infection 4 (2.25%), 136 (76.4%), 22 (12.36%), and 1 (0.56%) of the genotypes were immune, resistant, intermediate and susceptible to two or more isolates, respectively. In addition, Coatez *Yr15* and Avocet *Yr9* were immune to isolate 1. Furthermore, the additional component of the study was targeted to the study of the genetic architecture of adult plant resistance to yellow rust in 178 wheat association panels. The panel was phenotyped for yellow rust adult-plant resistance at three locations. Phenological, yield, yield-related and agro-morphological traits were recorded. The association panel was fingerprinted with

genotyping-by-sequencing (GBS) platform, and a total of 6,788 polymorphic SNPs were used for genome-wide association analysis (GWAS) to identify effective yellow rust resistance genes. The marker-trait association (MTA) analysis was conducted using Genome Association and Prediction Integrated Tool (GAPIT). The broad-sense heritability for the considered traits ranged from 74.52 to 88.64%, implying the presence of promising yellow rust resistance alleles in the association panel that could be deployed to improve wheat resistance to the disease. The overall linkage disequilibrium (LD) declined within average physical distance of 31.44 Mbp at $r^2 = 0.2$. MTA analysis identified 148 loci significantly ($p = 0.001$) associated with yellow rust adult-plant resistance. Most of the detected resistance quantitative trait loci (QTLs) were located on same chromosomes as previously reported for yellow rust resistance and mapped on chromosomes 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 6A, 6B, and 7A and 7D. Nevertheless, 12 of the discovered MTAs were not previously documented in the wheat literature, suggesting that they could represent novel loci for stripe rust resistance. Zooming into the QTL regions in International Wheat Genome Sequencing Consortium (IWGSC) RefSeq Annotation v2.1 identified crucial disease resistance-associated genes that are key in plants' defence mechanisms against pathogen infections. The detected QTLs will be helpful for marker-assisted breeding of wheat to increase resistance to stripe rust in Ethiopia and beyond. However, the efficacy of newly found QTLs need functionally confirmed before they can be used for marker-assisted selection

Keywords: Coefficient of infection, Hexaploid wheat, Marker trait association, Genetic variability, Genome wide association study, Heritability, Linkage disequilibrium, Novel loci, Population structure, *Puccinia striiformis*, Quantitative trait loci, SNP marker, Yr genes

CHAPTER ONE

INTRODUCTION

1.1. General introduction

Wheat is one of the major staple food crops of the world, providing 21% of the total energy and 20% of the protein demand for about 4.5 billion people globally (Ramadas et al., 2019). In 2021, about 221 million ha of the world was covered with wheat, with a total production and productivity of 784.91 million tons and 3.5 tons/ha, respectively (FAO, 2023). Current global wheat production involves bread wheat (*Triticum aestivum* L., $2n = 42$ with large genome size = 17Gb), covering 95% of the global wheat cultivation and the remaining 5% is covered by Durum wheat (*Triticum durum*, $2n = 28$ with genome size = 12Gb) and others (Patricia et al., 2019). Wheat is one of the globally produced and marketed cereal crops, which covers 15% of the total sowing areas of cereal crops in the world (FAOSTAT, 2023). Since 1991, the amount of wheat consumed in Sub-Saharan Africa (SSA) has significantly increased due to rising urbanization (Wudil et al., 2022). The situation has resulted in a change in people's dietary preferences from eating grains such as maize, sorghum, and millet to wheat and rice, as well as tuber crops like cassava, sweet potato, and yam (Noort et al., 2022). The Sub-Saharan Africa region imports more than 15 million tons of wheat grain each year, as the region's local wheat output has fallen short to keep up with the rising demand (Listman, 2019). For example, Africa imported around 54.8 million metric tons of wheat in the trade year 2021/2022 (Statiata, 2022). By 2025, wheat consumption in Africa is projected to reach 76.5 MMT, of which 48.3 MMT, which accounts for 63.3% of wheat demand should be covered through imports (Silva et al., 2023).

Next to South Africa, Ethiopia is the second-largest wheat producer in Africa in (FAO, 2017). In Ethiopia, bread wheat is an important staple crop, especially in urban areas, for many Ethiopians, making up almost 15% of the nation's more than 90 million population daily calorie consumption (FAOSTAT, 2023). It is also used as animal feed and for income generation (FAO, 2018). Furthermore, the importance of wheat is not only for making bread, biscuits, and pastry products but also for the production of starch and gluten (Hanson, 2022). In the country, wheat is one of the strategic food security crop (Bezabeh et

al., 2015) ranking fourth after teff (*Eragrostis tef*), maize (*Zea mays*) and sorghum (*Sorghum bicolor*) in area coverage and third after maize and teff in total production (CSA, 2019). In 2021, about 1.95 million ha of land was covered with wheat resulting in total national production of 5.2 million tons (FAOSTAT 2021). The major wheat-growing areas in Ethiopia are located between 6 and 16° N and 35 and 42° E and at altitudes ranging from 1500 to 3000 meter above sea level (masl). The most suitable areas for wheat production, however, fall between 1900 and 2700 masl. Furthermore, the central highlands, south-eastern and northwest parts are main wheat-growing areas in the country. In terms of regional contribution, the production of wheat originates from Oromia (57.4%) and more than 41% of the annual wheat production comes from only three areas in Oromia. Irrespective of the significant increase in average for wheat cultivation and production in Ethiopia, the national average of wheat productivity in stands at 2.7 t ha⁻¹, far lower than the global average of 3.6 t ha⁻¹ resulting in a production deficit to meet the rising local demand (Gemechu and Tadese, 2018). In which, Ethiopia satisfies 25-35% of its domestic wheat demand through commercial imports and food aid (Agriculture Global Practice, 2018). Ethiopia is the largest wheat producer in East Africa, with about 65% share of the total wheat production in sub-Saharan Africa. The area under wheat increased from about 1.5 million hectares in 2010 to 2.5 million hectares in 2023 (CIMMYT, 2023). More importantly, the productivity increased from 1.8 tons per hectare to about 3 tons per hectare in the same period, implying an increase of about 5% per annum in productivity.

1.2 Background of the study

Improving wheat production and productivity involves exploring the available genetic resources and their wise management. A systematic evaluation of various agro-morphological traits thus enables to exploit the genetic potential of different genotypes. According to Dargicho et al., (2015) evaluation of germplasm using agro-morphological variation could make it possible to understand genetic diversity and segregations of morphological traits, which are essential for genetic improvement. The description of the morphological traits is also significant for genetic diversity analyses (De Vita et al., 2010). Consequently, genetic variability, heritability and GxE studies among bread wheat genotypes based on quantitative traits were estimated. In breeding programs, the choice of

parents has ultimate importance for effective selection, while information on the nature and magnitude of variation in populations, the association of traits with grain yield and association among traits are essential. Different statistical analyses, such as cluster analysis, principal component analysis, correlation analysis and path coefficient analysis can be used to reveal associations between yield and other agro-morphological traits. These methods enable better understanding of germplasm's performance over several environments, and selection of stable and high-yielding genotypes (Yusuf et al., 2016). Since the performance or yield of each germplasm in any environment is a sum of environment (E), germplasm (G), and germplasm by environment interaction (GEI), additive main effects and multiplicative interactions (AMMI) and genotype environment interaction (GGE) biplot models are powerful tools commonly used for effective analysis and interpretation of multiple environment data (Samonte et al., 2005). Meanwhile, AMMI and GGE pertain to any two-way data matrices and such data emerge from many kinds of experiments, AMMI and GGE have broader relevance for agricultural researchers (Gauch, 2006; Mohibullah et al., 2013). Genotype-environment interaction is frequently tested by breeders for discrepancy ranking of germplasm yields in variable environments (Ahmadi et al., 2012).

Moreover, knowledge of the genetic diversity of a crop helps breeders to choose desirable parents for breeding programs and gene introgression from diverse germplasm to maintain sustainable crop productivity. As a result, plant breeders can develop new and improved cultivars with desirable characteristics including high yield potential, large seed, biotic stress resistance (disease and insect resistance) as well as tolerance to abiotic stresses like drought, cold and salinity (Allard, 1999; Haussmann et al., 2004). Furthermore, the more diversified the germplasm, the more likely it is to exploit high heterotic crossings and wide diversity in segregating generations during genetic improvement (Vermal, 2013). In addition, to assess genetic diversity DNA markers can assist in identifying and selecting the most genetically varied individuals for breeding programs.

DNA markers are commonly employed to discover genetic variation across plant genotypes that are resistant to environmental change, which can be exploited to select and produce new varieties with enhanced attributes. Breeders may make tasteful judgments about which genotypes to crossbreed by examining the DNA markers, resulting in the creation of more

hardy and adaptive plants. Molecular marker-based characterization does not require previous pedigree information (Frisch et al., 1999), and it has played a crucial role in the conservation, and use of plant genetic resources in trait improvement programs for various crops (Tirfessa et al., 2020). So far, several DNA markers such as restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), inter simple sequence repeat (ISSR), simple sequence repeat (SSR), and single nucleotide polymorphism (SNPs) have been widely used to address challenges that occur in changing ecology and agriculture. Inter Simple Sequence Repeat (ISSR) markers are among the molecular markers that are extensively used in various plant research studies for the evaluation of genetic variability within and among populations in several plant species including wheat (Najaphy et al., 2011; Najaphy et al., 2012; Ng and Tan, 2015; Rafiq et al., 2016). ISSR markers are preferable because they are highly polymorphic, more accessible, do not require preexisting sequencing information, and have good repeatability (Vijayan, 2005). Furthermore, ISSR markers are readily scaled up to evaluate huge sample quantities, making them perfect for exploring genetic variation on a larger scale. In addition, the use of highly polymorphic markers enables a more complete knowledge of population structure and evolutionary connections across distinct populations or species. ISSR markers, on the other hand, have the drawback of being susceptible to scoring mistakes due to band size changes, as well as the possibility of results not being reproducible between laboratories. Furthermore, ISSR markers may give less information on individual gene activities than other molecular markers such as SSRs or SNPs.

On the other hand, fungal diseases such as stripe rust (also known as yellow rust), stem rust, leaf rust, septoria tritici blotch (STB) are the major bottlenecks for wheat production in Ethiopia. If not controlled, rust diseases have the potential to cause 50-100% wheat yield loss (Chen, 2005) with an estimated cost of 5.5 billion USD per annum globally (Beddow et al., 2015). Stripe rust, often known as yellow rust caused by the rapidly evolving pathogens *Puccinia puccinia striiformis* f. sp. *tritici* is a devastating wheat disease that affects cooler (2-15 °C) wheat-growing regions of the world (Roelfs et al., 1992). It continues to be a significant global limitation on wheat production. It affects leaves, where the ensuing damage to photosynthetic tissues causes a reduction in the efficiency of light absorption and radiation (Bouvet et al., 2022). Furthermore, yellow rust limits yield by

reducing the green leaf area, which supplies sugar to the developing seed. This is because flag leaves and second leaves are the most important leaves for producing sugar for the developing grain (Murray et al., 2005). As flag leaf contribution is high for grain filling, its infection with stripe rust results in significant yield loss (Marsalis and Goldberg, 2006). Beside, yellow rust spores migrate quickly and may travel long distances to produce diverse populations making control of the distribution of the disease difficult (Vergara-Diaz et al., 2015).

In Ethiopia, *P. striiformis* is the most common rust pathogen, causing considerable wheat yield losses of up to 100% in the worst seasons (Tadesse et al., 2018). Crop yield loss due to stripe rust, necessitate well-organized plant disease management and control (Sarrocchio and Vannacci, 2018). However, broad use of fungicides to treat fungal diseases has the potential to affect the environment and animal welfare (Bhandari et al., 2019). These pollutants can contaminate water supplies and soil, endangering aquatic ecosystems and upsetting natural ecological balance. Meanwhile, the most cost-effective technique for managing yellow rust is the development of resistant cultivars, which also decreases negative environmental and human health effects by employing fewer fungicides (Chen, 2005; Hansona et al., 2016). Screening and breeding plant varieties with natural resistance to fungal infections are part of the process of developing resistant cultivars, which reduces the need for chemical fungicides. Varietal resistance, on the other hand, can be easily overcome due to the introduction of novel *P. striiformis* races or mutations (Wellings, 2011). Since the production of resistant cultivars is the most effective, economical, and environmentally safe management approach (Chen, 2005), effective resistance breeding necessitates accurate postulation of pathogen virulence patterns as well as the discovery and use of novel resistance genes that outperform the basic virulent races (Admassu et al., 2012). Besides, integrated disease management measures for stripe rust include timely fungicide applications, resistant crop varieties, and cultural practices such as crop rotation, which help to reduce the spread of the disease and minimize yield losses in wheat and barley crops.

The idea of a gene-for-gene relationship is also founded on the recognition of particular pathogen avirulence genes by corresponding plant resistance genes. According to the

presence or absence of particular gene pairs, it describes how a pathogen's interaction with a plant can result in disease susceptibility or resistance. This can be utilized to categorize genes that are present and active during the seedling stages (Flor 1971). Resistance genes from seedlings are frequently active throughout the adult plant stage and are classified as race-specific resistance (Lagudah 2010). These scales give a consistent method for evaluating the efficacy of various resistance genes against yellow rust infestations. Breeders can produce more permanent and effective resistance in new crop types by intentionally selecting and combining resistance genes. This technique can help to reduce the impact of changing rust pathogen populations and assure long-term crop protection (Zhang et al., 2022). Resistant (R) genes in the host plant and avirulent (Avr) genes in the wheat rust pathogen are responsible for the transmission of resistance to these infections in wheat genotypes. The presence of Avr genes in the wheat rust pathogen causes a unique immunological response in the host plant, resulting to infection resistance. Multiple studies have used gene postulation to uncover stripe rust resistance genes in wheat lines from Nepal, Denmark, China, and Ethiopia (Dawit et al., 2012). Scientists were able to identify the genes responsible for wheat rust resistance by testing wheat genotypes and wheat differential sets (wheat lines with known yellow rust resistant genes) in different countries (Xiaodan et al., 2011). The host plant-pathogen gene-for-gene connection is therefore critical for the plant's defense mechanism.

Besides, due to the ongoing development and selection of rust races, it is always preferable to look for additional sources of potent rust resistance genes. As a result, it requires the discovery and use of new resistance genes to defeat the dominant pathogenic races. As of 2017, 67 all-stage resistance (seedling and adult-plant resistance) genes and 80 race-specific/seedling yellow rust resistance genes (Yr) have been reported (Wang and Chen, 2017). According to Kankwatsa et al., (2017) and Yuan et al., (2018), adult plant resistance to pathogen mixtures is thought to be reliable and effective in field conditions. Since conventional breeding methods have been viewed as slow and ineffective despite their significant contributions to crop improvement (Liu et al., 2017), molecular markers are now often utilized in plant breeding to speed up crop improvement efforts. As a result, the effectiveness of breeding disease-resistant wheat can be increased by identifying molecular

markers that are strongly connected to Yr genes, or quantitative trait loci (QTLs) (Miedaner and Korzun, 2012; Ayana et al., 2018).

A genome-wide association study (GWAS) is a powerful, fast, and economical approach to determining genomic regions associated with complex quantitative phenotypic variation (Yuan et al., 2018). GWAS enables us to dissect genes or QTLs underlying important traits using SNPs derived from whole-genome sequencing (Liu W.Z. et al., 2017; Zia et al., 2020; Ali et al., 2021; Nadeem et al., 2021). Hence, its advancement is correlated with the development of high-throughput sequencing technology (Huang et al., 2019). Furthermore, genotyping-by-sequencing (GBS) is a reasonably priced genetic screening method for discovering novel SNPs. GBS includes restriction digestion followed by high-throughput sequencing of a subset of a complex genome, which enables the generation of high-density SNPs (Bernardo et al., 2015). Moreover, GWAS has been used to dissect disease resistance's genetic foundations in a range of plant species, including maize (Rashid et al., 2018), arabidopsis (Rajarammohan et al., 2018), sorghum (Adeyanju et al., 2015), and soybean (Passianotto et al., 2017). For example, leaf rust, stem rust, stripe rust, and septoria tritici blotch resistance have all been studied in wheat using the GWAS technique (Kidane et al., 2017; Odilbekov et al., 2019; Mekonnen et al., 2021).

1.3 Statement of the problem

Yellow rust is the most widespread disease in Ethiopia, as a result of which 36 to 100% wheat yield loss has been reported (Badebo and Bayu, 1992; Ayele and Muche, 2019; Hailu and Fininsa, 2009). Yellow rust can rapidly spread under favorable environmental conditions, leading to severe yield losses and economic hardship for farmers in the highland regions. In the highlands and mid-altitude regions of Ethiopia, yellow rust was to blame for the collapse of the dominant wheat varieties, including Laketch in 1977, Dashen (a well-liked high-yielding variety with the Yr9 gene) in 1988 and 1994, Wabe in 1998 (Badebo and Bayu, 1992), and Galema and Kubsa in 2010 (Tadesse et al., 2018). Likewise, in 2010, stripe rust epidemics occurred in all major wheat-growing areas of Ethiopia, causing large yield losses (Solh et al., 2012; Dembel, 2014). The stripe rust epidemics in 2010 further exacerbated the economic losses faced by farmers in Ethiopia. These varieties were swiped out to yellow rust, making them unable to withstand the rapid spread of the disease. As a

result, farmers faced significant economic losses and had to find alternative wheat varieties that were resistant to yellow rust.

Besides, the gene-for-gene relationship identifies pathogen avirulence genes and plant resistance genes, determining disease susceptibility or resistance. This helps to categorize genes which are active at the seedling stages and race-specific resistance. Breeders can develop permanent resistance by intentionally selecting and combining resistance genes disrupted by different rust pathogen races. Resistant (R) genes in the host plant and avirulent (Avr) genes in the wheat rust pathogen transmit resistance, resulting in unique immunological responses in the host plant. This connection is crucial for the plant's defense mechanism against yellow rust infestations. On the other hand, new stripe rust races are moving and spreading throughout the world's wheat-producing regions, necessitating the identification and transfer of novel sources of resistance genes. Since they may defeat previously resistant cultivars, these new yellow rust races pose a substantial danger to global wheat output. As a result, it is critical to constantly seek out and uncover new sources of resistance genes capable of efficiently combating these developing races. Furthermore, the incorporation of these resistance genes into commercially viable wheat cultivars is critical for long-term protection against yellow rust spread and food security. Given the pathogen's growing economic relevance in Ethiopian wheat production system, more understanding is critical for planning and implementing long-term management tactics (Hundie et al., 2019). Similarly, without knowledge of the resistance status of commercial wheat cultivars, which is critical for identifying potential sources of yellow rust resistance, it is difficult to replace vulnerable cultivars with resistant genotypes. Thus, the current study was carried out to better understand the virulence Variability among four Ethiopian *P. striiformis* isolates acquired from Arsi and Bale areas, which are the main wheat-growing regions of the country.

Principally, GWAS, a way to find genomic areas associated with complicated quantitative phenotypic variance, enables the dissection of genes or QTLs underpinning significant characteristics utilizing whole-genome sequencing. Along with GBS, it is a genetic screening method for discovering novel SNPs and provides a comprehensive approach to understanding their role in shaping diversity. Nevertheless, the application of the GWAS

technique along with GBS in breeding bread wheat resistant to stripe rust is missing in Ethiopia (Mengesha, 2020). Hence, the present study mainly targeted to determine the genomic architecture of adult-plant resistance of 178 bread wheat genotypes resistant to stripe rust in Ethiopia, which could be used in future marker-assisted breeding programs of wheat against the disease.

1.4 Objectives

1.4.1 General objective

- To explore genetic diversity, heritability, GxE interactions and genomic regions associated with stripe rust (*Puccinia striiformis* f.sp. tritici) resistance in bread wheat genotypes

1.4.2 Specific objectives

- ❖ To investigate genetic diversity and population structure analysis of bread wheat genotypes using ISSR markers
- ❖ To evaluate genetic variability, heritability and genotype environment interaction of bread wheat genotypes
- ❖ To identify virulence variability of Ethiopian stripe rust isolates and seedling resistance in bread wheat genotypes
- ❖ To investigate genomic architecture of adult-plant resistances to stripe rust association panel and important agronomic traits in bread wheat association panel using high-density SNP markers

1.5 Significance of the study

Finding of this study is critical for establishing more successful breeding techniques to increase the productivity and resilience of Ethiopian bread wheat. The genetic diversity and population structure of bread wheat genotypes using inter-simple sequence repeat (ISSR) markers could subsequently be utilized to selectively develop cultivars with desired traits like disease resistance or drought tolerance. Coupled with, the variability, heritability, and genotype-environment interaction of those bread wheat genotypes investigated in this study looked at how genetic variables impact the observed variability in yield performance. Likewise, the correlation between agro-morphological traits can show substantial connections between agro-morphological traits and grain yield. As a result, these findings

are significant in understanding the factors that contribute to the yield performance of bread wheat genotypes. By examining the variability, heritability, and genotype-environment interaction, researchers can gain insights into how genetic variables influence yield outcomes. As well, the identified correlations between agro-morphological traits and grain yield provide valuable information for breeders and farmers to select and cultivate high-yielding wheat varieties.

P. striiformis isolates virulence variability identified race-specific stripe rust resistance in bread wheat genotypes under greenhouse conditions help to understanding the mechanisms of host-pathogen interactions and developing effective disease management strategies. Researchers can establish which individual genes in bread wheat genotypes provide resistance to stripe rust races by investigating the pathogenicity variability of *P. striiformis* isolates. This understanding is critical for breeding projects to generate resistant wheat varieties and reduce the severe impact of the disease on food security. By detecting the specific genes responsible for yellow rust resistance, breeders can develop new wheat varieties with enhanced resistance to this pathogen, leading to increased yields and improved food security. Indeed, marker trait associations, are significant to further understanding the genetic basis of stripe rust resistance in bread wheat. Marker trait associations provide valuable insights into potential targets for breeding programs aimed at developing resistant wheat varieties. Additionally, their discovery highlights the importance of continued research and exploration to uncover additional novel loci that can contribute to improved disease resistance in wheat crops.

Largely, this knowledge can also help in the development of molecular tools, including diagnostic tests that can detect resistant genotypes quickly and correctly, allowing breeders to make tasteful decisions regarding disease management strategies. Accordingly, the findings will be helpful in upgrading the small scale farmer's by increasing wheat productivity by increase the domestic production and to reduce the wheat imports which play well-intentioned role in relation to foreign currency.

CHAPTER TWO

LITERATURE REVIEW

Triticum aestivum, or bread wheat, belongs to the order Poales, family Poaceae (Gramineae), tribe Triticeae, and genus *Triticum* (National center for biotechnology information, 2024). *Triticum* plants have the following physical characteristics: a short ligule and hairy spikelets, as well as a smooth, bald, hollow culm that ranges in height from 0.7 to 1.6 meters. Pithy fillings are less prevalent than hollow culms. The ears' rachis is brittle or stiff. Typically, they are four-sided. The spikelets include two to five florets. Each floret produces one grain (caryopsis), indicating that it is distichous. *T. aestivum*, for example, has keeled glumes on the top side, as well as serrated lemmas that are long and either bearded or unbearded.

Wheat is a staple grain that has played an important part in human history for thousands of years. It is valued for its high protein content, which plays a vital role in human nutrition. It serves as a substantial source of essential amino acids, including lysine and tryptophan, which are often limited in other cereal crops (Shewry and Hey, 2015). Moreover, wheat is rich in dietary fiber, vitamins, and minerals. Based on its end use, wheat is categorized and consumed in two basic categories: bread (*Triticum aestivum*) and durum (*Triticum durum*) wheat. Due to its high gluten content, bread wheat is often used to make bread, pastries, and other baked items (Goel et al., 2021; Šmídová et al., 2022). On the other hand, durum wheat is mostly used to make pasta, couscous, and some varieties of bread that require a thicker texture. Both kinds offer distinct gastronomic sensations and contribute to the market's vast spectrum of wheat-based items (Sissons, 2022). Because the species are recent polyploids, most genes in current wheat are present in two or three functional copies, with over 96% sequence homology (Pourkheirandish et al., 2015). Since there is significant sequence similarity between genes, bread wheat and durum wheat can be interchanged in specific culinary items. However, tiny variances in its genetic composition result in texture and flavor variations, giving each type of wheat its own features (Marina et al., 2018). Moreover, bread wheat is the most frequently cultivated crop in the world, accounting for around 95% of total wheat production; Durum wheat and ancient wheat such as *Triticum dicoccum* account for the remaining 5% (de Sousa et al., 2021). Other wheat cultivars

(einkorn (*Triticum uratra*), emmer (*Triticum dicoccoides*), and spelt (*Triticum spelta*)) are still grown in some regions of the world and used in traditional and specialized baking (Friedrich et al., 2015; Roumia et al., 2023). However, due to its high protein content and gluten strength, which give pasta its characteristic chewy texture and capacity to keep form throughout cooking, durum wheat remains the favored choice for creating pasta (Raimondo et al., 2007). Furthermore, the golden hue of durum wheat lends visual appeal to pasta dishes, making it a popular option in Mediterranean and Italian cuisines (Nilusha et al., 2019).

On the other hand, bread wheat is appropriately referred to as the "golden grain" (Mohan and Malleshi 2006), since it is one of the world's most frequently farmed cereal crops, ensuring food security for a large section of the world's population. Bread wheat's development and domestication have been important elements in its success as a staple food source. In addition, bread wheat has acceptable processing qualities that make it an excellent choice for baked foods, in addition to its nutritional content. Wheat gluten's unique viscoelastic qualities allow the dough to rise and achieve a desirable texture, leading to the light, fluffy structure of bread (Šmídová et al., 2022). This property enables bakers to produce a diverse range of items, such as numerous types of bread, cakes, and pastries. Furthermore, bread wheat is very adaptable to a wide range of environmental conditions, making it appropriate for production in a variety of locations around the world. Its tolerance for a wide variety of temperatures, rainfall patterns, and soil types has contributed to its widespread distribution in temperate and subtropical locations (Reynolds et al., 2009). Moreover, it is a significant calorie source in Ethiopian diets, particularly in rural areas. Wheat accounts for 9-20% of Ethiopian calories ingested, depending on the source, and a bigger part of daily caloric intake among communities (Bezabeh et al., 2015; Dibaba, 2019). Additionally, bread wheat accounts for over half of the planted area and is often farmed in the highland and semi-highland districts of Oromia, Amhara, Tigray, and other regions of Ethiopia. Bread wheat is grown at higher altitudes and on better-drained soils than durum wheat (Jeffrey et al., 2023). Moreover, bread wheat is popular in agro-industries because of the smaller size of the seeds and weight, which allows it to be broken down into finer flour and has a softer texture (Pang et al., 2021).

Understanding the biology of bread wheat, including its genome, and genetic diversity, is critical for increasing crop yields, generating disease-resistant types, and ensuring global food security (Gegas et al., 2010). Following germination, the seedling grows into an adult plant through the stages of vegetative, blooming, and grain maturity (White and Edwards, 2008). Temperature, photoperiod, water availability, and nutrient delivery all influence these growth stages and, as a result, the eventual output (Mikhail et al., 2009; Guarin and Asseng, 2022). On the other hand, genetic diversity is an important feature of bread wheat biology that helps crop improvement. Since diverse genetic resources can improve yield potential, disease resistance, and stress tolerance, plant breeders have used traditional breeding strategies, including crossbreeding and selection, to generate high-yielding and adaptable wheat cultivars (William and Michael 2014). Furthermore, new molecular breeding tools, including marker-assisted selection (Vagndorf et al., 2018; Song et al., 2023), genomic selection (Manzoor et al., 2022), and gene editing (Kang et al., 2020), have transformed the process of bringing specific improvements into bread wheat cultivars (Shiferaw et al., 2013; Aloisi et al., 2023). This knowledge can then be used to develop breeding strategies aimed at improving these traits in future wheat varieties. Additionally, studying the growth stages of bread wheat helps to optimize cultivation practices and ensure optimal crop management, ultimately leading to increased productivity and sustainability in wheat production. Therefore, its unique genomic structure and knowledge of its genetic variation provides insights into its flexibility and possibilities for improvement (Bapela et al., 2022; Niu et al., 2023).

2.1 Evolution and domestication of bread wheat

The grass family Poaceae developed 50-70 million years ago (Mya) (Huang et al., 2002), while the subfamily Pooideae, which includes wheat, diverged around 20 Mya (Inda et al., 2008). The initial cultivation of diploid and tetraploid wheat is considered to have occurred some 10,000 years ago in the fertile crescent of the Middle East today's Jordan, Syria, Iran, Iraq and Turkey (Dubcovsky and Dvorak, 2007; Office of the Gene Technology Regulator, 2017). Bread wheat is the result of the natural hybridization of three ancestral species: Einkorn wheat (*Triticum uratra*), Emmer wheat (*Triticum dicoccoides*), and Goatgrass (*Aegilops tauschii*) (Marcussen et al., 2014) (Figure 1). Since early farmers understood the

advantages of wheat cultivation, which led to the intentional selection and propagation of plants with desirable traits such as larger grain size, non-shattering spikelets, and higher production potential (Feldman and Levy, 2023), these initiatives prepared the way for wild wheat to be domesticated into a more productive and reliable crop. The first cultivated wheat varieties were essentially landraces selected by farmers from wild populations, presumably due to higher production and other relevant traits. Since domestication was also linked to the selection of desired traits that distinguished them from their wild relatives, the development of non-shattering seed and the rise in grain size were the two most essential features in the evolution of bread wheat (Guo et al., 2023). The former characteristic (a hallmark of domestication) hinders natural seed distribution and allows humans to harvest and collect the seed at the optimal time (Nancy 2010; Maity et al., 2021), because the spike shatters at maturity, resulting in seed loss during harvesting. As a result, farmers prefer less shattering because it is a critical characteristic for guaranteeing seed distribution (Nalam et al., 2006). The second distinguishing feature is the transition from hulled forms, in which the glumes attach closely to the grain, to free-threshing naked forms (Shewry, 2009).

Furthermore, Gegas et al., (2010) provided strong evidence that grain size and shape are traits in which wheat domestication resulted in a shift from the production of a relatively small grain with a long, thin shape to a more uniform, larger grain with a short, wide shape. These findings highlight the complicated history of domesticated wheat evolution, implying that multiple features (including some that are closely related) evolved independently at various phases. Except for variety of bread wheat, all cultivated forms of diploid, tetraploid, and hexaploid wheat have a robust rachis. Similarly, early domesticated types of einkorn, emmer, and spelt are all hulled, while modern tetraploid and hexaploid wheat varieties are bare (Dubcovsky and Dvorak, 2007). Whereas einkorn and emmer were domesticated from natural populations, bread wheat has only existed in culture, resulting from the hybridization of cultivated emmer with the unrelated wild grass *Aegilops tauschii*. This hybridization most likely occurred numerous times separately, with farmers selecting the novel hexaploid for its superior features.

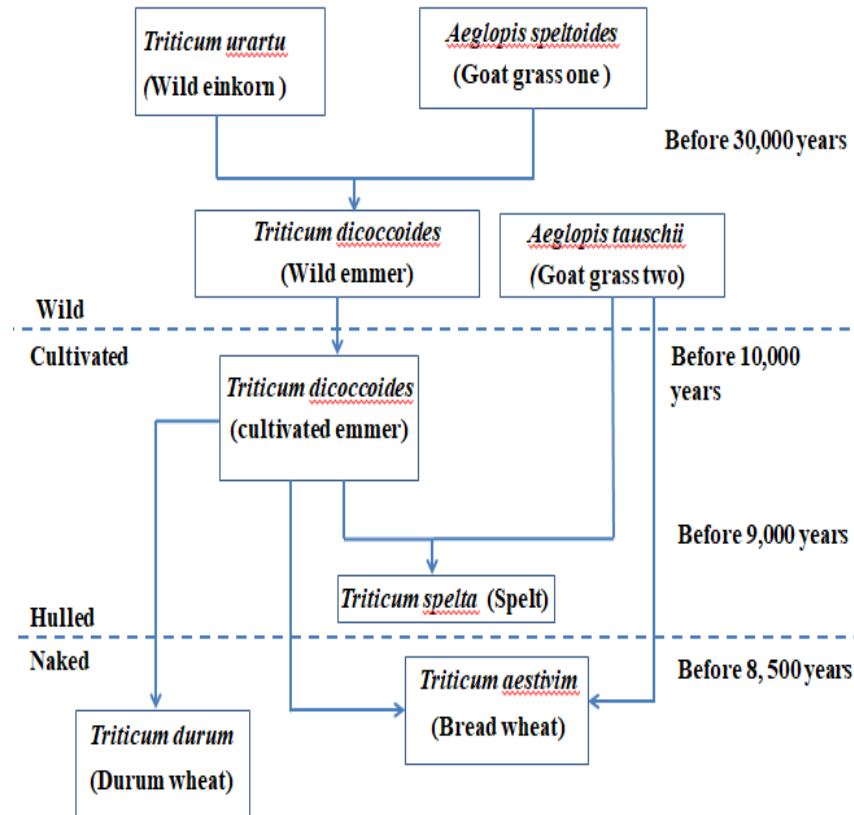


Figure 1. Evolution and domestication of bread wheat (source; Tadesse et al., 2018)

Bread wheat is a hexaploid with three sub-genomes (Linyi et al., 2015; Li, Yang et al., 2019) in which each sub-genome has seven homologous groups where each homologous group has three closely linked chromosomes (Dubcovsky and Dvorak, 2007). The bread wheat genome is extremely complex, with three closely linked and independently maintained sub-genomes identified as A, B, and D (IWGSC, 2018). Its growth and development can be separated into various stages. Understanding the content and function of these subgenomes is critical for unraveling the genetic complexity of bread wheat and enhancing its agronomic characteristics. The three subgenomes play an important role in shaping bread wheat's genetic variety, flexibility, and overall productivity (Kong et al., 2023). Each subgenome contains distinct alleles that contribute to a variety of agronomically significant properties, such as yield, disease resistance, and abiotic stress tolerance. Advanced molecular approaches, such as genomics, have been used in studies to analyze the specific contributions of these subgenomes. The bread wheat reference genome (IWGSC RefSeq v1.0), transcriptome, and proteome databases have greatly benefited the

discovery and study of genes and proteins that are unique to each subgenome, offering insights into their specific activities and contributions to wheat biology (Ling et al., 2018). Furthermore, the availability of these datasets has accelerated the development of molecular breeding approaches for improving bread wheat agronomic characteristics (Gil et al., 2020).

Regarding the origin and evolution of the bread wheat sub-genomes, it appears that *T. urartu* (2n = 14) is the donor of sub-genome A (Levy et al., 2022), (Figure 2). On the other hand, the origins of sub-genomes B and D in bread wheat have been a subject of debate among researchers. Some studies suggest that sub-genome B originated from *Aegilops speltoides* (Feldman, 2001), while others intend that it came from *Aegilops tauschii*. However, recent extensive studies on the origin and evolution of the bread wheat sub-genomes have shown that sub-genome B originated from *Aegilops speltoides* (Azat et al., 2023). Similarly, the exact donor of sub-genome D is still uncertain, with some studies pointing towards *Aegilops tauschii* and others suggesting a different species as the potential donor. Though, *Ae. tauschii* (synonyms: *T. tauschii*, *Ae. squarrosa*) has been identified as the donor of sub-genome D (Azat et al., 2023). This has recently been confirmed through analysis of the DNA sequences of two genes, namely, *Acc-1* (plastid acetyl-CoA carboxylase) and *Pgk-1* (plastid 3-phosphoglycerate kinase) (Huang et al., 2002; Feldman and Levy, 2023).

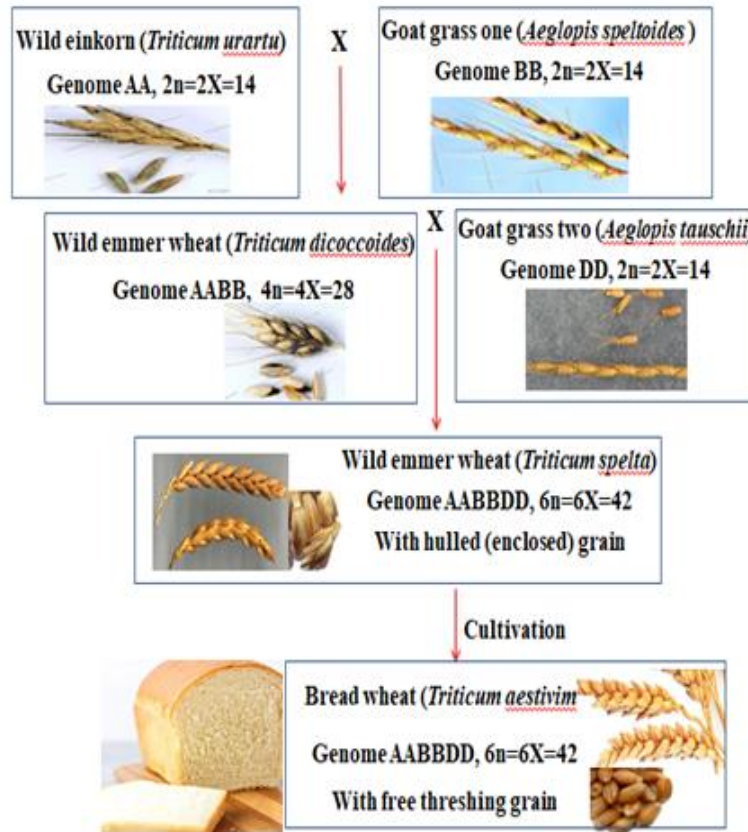


Figure 2. Evolution of the three Sub-genomes of Bread Wheat (source; Pourkheirandish et al., 2020)

2.2 Nutritional values of wheat

Cereals, particularly wheat, account for the majority of food aid (Jacqueline, 1999; USDA, 2015). This is because wheat is a good source of fiber as well as being higher in protein, most minerals, and vitamins B3 and B6 compared to rice or maize (Webb et al., 2011). In addition, wheat is rich in complex carbohydrates and provides sustained energy due to its high starch content (Kim and Kim, 2021). Since wheat is rich in fiber, which aids digestion and promotes gut health as well as reduce cardiovascular diseases (Obasi and Askepnde, 2023). Wheat is high in vitamins including a lot of B vitamins like thiamin, niacin, and folate (Shewry and Hey, 2015). Thiamin supports brain function and skin health; niacin promotes brain function and skin health; and folate is necessary for DNA synthesis and cell division (Delcour et al., 2012). Additionally, epidemiological studies provide substantial evidence that wheat intake is connected with a lower risk of chronic illnesses such as coronary heart disease, cardiovascular disease, type 2 diabetes, total cancer, and all-cause mortality

(Sang et al., 2020). However, it is crucial to remember that individual reactions to wheat consumption might vary, and some people may have unfavorable consequences such as gluten sensitivity, inflammation, and neurodegeneration.

Additionally, wheat contains vital nutrients such as iron, magnesium, and selenium. Iron is needed for the formation of red blood cells, whereas magnesium promotes bone health and blood pressure control (Javid-Iqbal et al., 2022). Besides selenium is an antioxidant associated with a decreased risk of certain malignancies (Shewry et al., 2022). Chemically, one hundred grams of wheat can have 339 kcal of energy, 10.3 g of protein, 49 mg of calcium, and 1.5 mg of iron (Tibebu, 2017). Although wheat contains a range of essential components, its nutritional value varies based on wheat variety, growing conditions, and processing methods. Nonetheless, eating wheat products as part of a well-balanced diet can help to meet daily nutritional needs.

2.3 Wheat production and constraints in Ethiopia

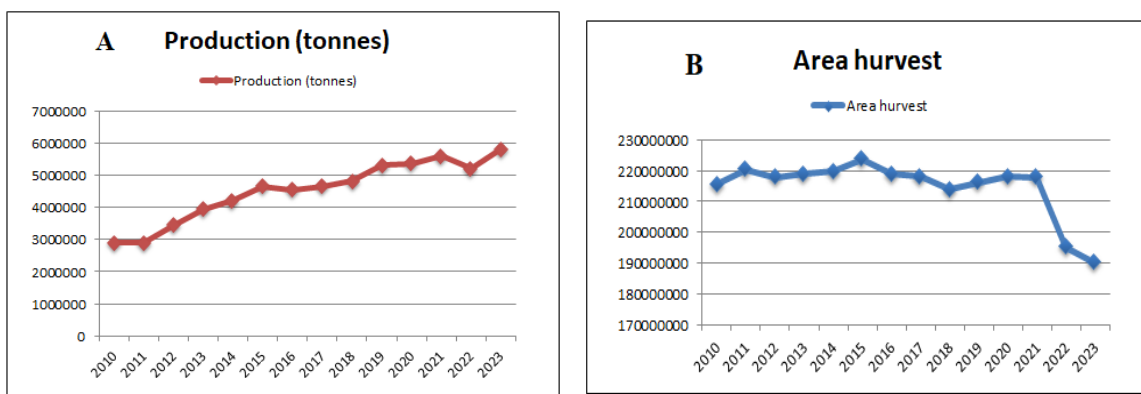
2.3.1 Wheat production in Ethiopia

Agriculture is generally known to dominate the economies of several African countries, including Ethiopia. It is a key raw material provider for the food processing, beverage, and textile sectors. In Ethiopia, agriculture employs more than 85% of the labor force and generates 90% of export revenues (Alemu et al., 2010; Welteji et al., 2018; Wendimu and Moral, 2021). Unambiguously, wheat is the world's most significant cereal crop; including Ethiopia (Kifle, 2016) with an average yield of 3.05 t/ha metric tons per hectare (FAOSTAT, 2023). Furthermore, Ethiopia is the second leading producer of wheat in Africa next to South Africa, with about 36% of the Ethiopian population dependent on the grain as a staple crop (Amare, 2018). Wheat mostly grows in the Ethiopian highlands, which lie between 6 and 16° N and 35 and 42° E, at altitudes ranging from 1500 to 3000 m. The most suitable areas for wheat production, however, fall between 1900 and 2700m (Tefera et al., 2021; Alambo et al., 2022).

According to Goshu et al., (2019), Ethiopia ranks 31st in the world, with 420,000 tons produced on 1.7 million hectares of land. Ethiopia is one of Africa's leading wheat producers in 2017, with large-scale commercial farming as well as small-scale farming

contributing to the total production (Hei et al., 2017). Wheat, like any other agricultural crop grown in the country, is rain fed, with both large rains (meher) occurring from June to September and short rains (belg) falling from February to April. Almost the majority of the country's wheat production comes from the country's central, south-eastern, and northwest highlands. In terms of regional contribution, wheat output comes from Oromia (57.4%), Amhara (27%), SNNP (8.7%), and Tigray (6.2%) (Abate, 2018; Dibaba, 2019). Besides, the central highlands, North Shewa, West Shewa, Arsi, Bale are Ethiopia's key wheat-growing regions (Anteneh and Asrat, 2020).

According to FAOSTAT data of 2023, the average wheat production in Ethiopia was 3.05 t/ha (Figure 3 A). However, in some African nations, such as Egypt, in addition to the rained production system, large-scale commercial farms grow wheat under irrigation. This enables them to produce the appropriate quantity of wheat at the required quality for the market. This has allowed these countries to meet their domestic demand for wheat and even export surpluses to other regions. In contrast, Ethiopia's reliance on rained production limits its ability to consistently meet the growing demand for wheat, resulting in lower yields compared to countries with diversified production systems in recent years, Ethiopia has made efforts to improve its agricultural practices by implementing irrigation systems and promoting crop diversification. Promising outcomes in raising wheat yields and decreasing reliance on erratic rainfall have been demonstrated by these programs.



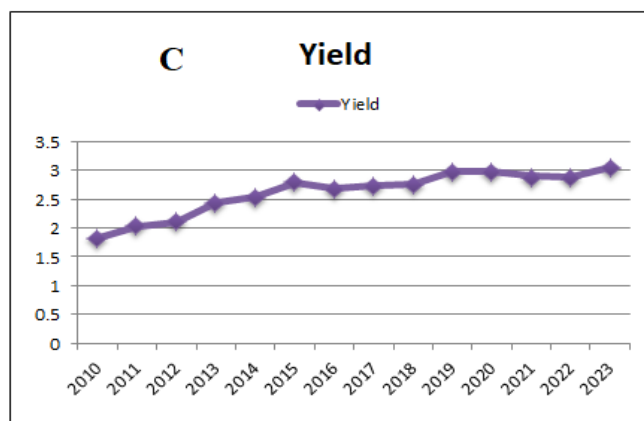


Figure 3. Status of wheat production (A), area coverage (B) and productivity /yield (C) from 2010 to 2023 (source: FAOSTAT, 2023 online report)

In Ethiopia, wheat production, area harvest, and productivity have increased over the last 12 years, from 2.92 to 5.58 million tones, 1.4 to 1.9 million hectare, and 2.03 to 3.05 tha^{-1} from 2010 to 2021 respectively (FAOSTAT, 2023) (Figure 3 A, B and C). This significant increase in wheat production area harvest and productivity can be attributed to various factors such as improved agricultural practices, and the adoption of high-yielding wheat varieties (Shikur, 2022). However, the current national average wheat production of 3.05 t/ha in 2023 is much lower than the global average of 3.6 tons per hectare, resulting in a production gap to meet rising local demand (Tesfaye, 2017). This production gap highlights the need for strategies to improve wheat productivity in order to meet the increasing demand. Implementing innovative farming techniques and utilizing advanced technologies could help bridge this gap and enhance wheat yields to meet local needs.

Moreover, Ethiopia's domestic wheat production can cover less than 65% of home demand, 26 % import, and 9% carryover from the country (Nicholas et al., 2015). This reliance on wheat imports not only puts a strain on the country's economy but also makes it vulnerable to fluctuations in international wheat prices. Lower productivity can be attributed to insufficient agricultural inputs, and biotic and abiotic stressors (Tadele, 2017), which hinder the efficiency and effectiveness of production processes, leading to lower overall production and productivity. Additionally, inadequate infrastructure and lack of proper training for farmers can also contribute to reduced productivity in agricultural systems (Zerssa et al., 2021). Despite these challenges, the Ethiopian government and other

stakeholders have taken initiatives to increase wheat yield in order to improve food security and reduce reliance on imports. Attempts have been made to enhance the use of improved varieties, implement modern farming practices, and offer farmers training and financial aid (Tadesse et al., 2021). Additionally, the government has also made investments in irrigation infrastructure development in order to mitigate the effects of drought and increase productivity (Adela et al., 2019). In this regard, the Ethiopian Agricultural Transformation Agency (ATA) has played a vital role by closely working with farmers to encourage the use of better seed varieties and farming methods. The collaborations between local research institutes, foreign organizations, and non-governmental organizations (NGOs) have also played an important role in increasing wheat productivity in Ethiopia. Besides, organizations such as the International Maize and Wheat Improvement Center (CIMMYT) have performed research to generate high-yielding, disease-resistant wheat varieties appropriate for Ethiopia's specific agro-climate. These efforts have significantly contributed to increasing wheat production in Ethiopia and improving food security for the population (Senbeta et al., 2023).

2.3.2 Wheat demand in Ethiopia

Ethiopia has faced challenges in meeting its domestic wheat demand due to a number of factors that have contributed to the country's increased consumption and reliance on wheat as a staple food. Primarily, population expansion and urbanization have had a big effect on raising Ethiopian wheat demand. As the world's population grows and more people relocate to cities, there is an increasing need for easy and easily accessible food options, with wheat-based goods being a popular choice (Alemu, 2010; Etminan et al., 2019; Herbert et al., 2020; Kihara et al., 2022). Second, shifting dietary tastes and lifestyles have led to an increase in wheat demand (Noort et al., 2022). Ethiopians are increasingly embracing Western-style diets that rely significantly on wheat-based items such as bread, pasta, and pastries as a result of rapid globalization and exposure to diverse culinary traditions (Cappelli et al., 2021). According to Mottaleb et al., (2021), Ethiopia has seen a large increase in wheat consumption in recent decades due to fast population expansion, urbanization, and changing food habits.

While wheat imports have met Ethiopia's immediate food needs, they also raise economic concerns. The high expenses of importing huge amounts of wheat put a strain on the country's balance of costs and foreign exchange reserves. Furthermore, variable global wheat prices and currency fluctuations might put further strain on the economy by altering import costs. Besides, the country's reliance on wheat imports has an impact on food security. Ethiopia's sensitivity to external shocks, such as changes in international market conditions or disruptions in transportation networks, highlights the importance of developing a more sustainable and robust domestic wheat production system.

2.3.3 Constraints of wheat production in Ethiopia

Wheat production is critical to assuring food security. However, factors such as lack of access to improved inputs such as quality seeds, fertilizers, and insecticides act as most significant obstacles to optimal wheat production (Nigus et al., 2023). In Ethiopia, as Tesfaye et al., (2017) demonstrated utilizing low-quality seeds has considerable impact on yield and overall productivity. The country's wheat production is also hampered by a lack of access to water resources during important growth stages because of total reliance on rainfed agriculture which is usually affected by erratic rainfall patterns. Furthermore, soil nutrient depletion and degradation pose considerable hurdles to Ethiopian wheat production (Wassie, 2020). The overuse of chemical fertilizers without suitable soil management measures reduces soil fertility and has a long-term impact on crop yields. In addition, inadequate market linkage and insufficient value chain systems, price swings, and poor storage facilities contribute to significant post-harvest losses, which are estimated to be between 2-20% of total production (Tadesse et al., 2015, Tadesse, Bishawand et al., 2018; Shikur, 2023). Pests and diseases such as aphids, Hessian flies, and rusts (stem, leaf, and stripe rust) also cause significant yield losses and are key restrictions to wheat production around the world including Ethiopia (Gadisa, 2019; FAO, 2016; Figueroa et al., 2018). The bread wheat improvement program in Ethiopia released over 50 varieties. However, their great producing potential and rust resistance will not survive long, owing to the yellow rust epidemics (Tolemariam et al., 2018). Yellow rust infections remained a serious biotic threat to wheat production in Ethiopia. Ethiopia has now reached the point where bread wheat

cannot be grown without the use of fungicides, particularly in wheat belt zones such as Arsi and Bale Zones (Delesa et al., 2020).

2.4 Genetic diversity of bread wheat

A crop enhancement scheme requires significant genetic variety, which is critical to examine trait variability and how a particular variable influences crop productivity. To guarantee successful selection, data on the type and extent of variation within the population, trait associations with yield and each other, and the influence of the environment on trait expression must be gathered (Raviteja et al., 2023). Besides, several morphological, biochemical and molecular approaches are available for analyzing genetic diversity in wheat germplasm. Different morphological and agronomic parameters, as well as pedigree information, have been used to assess wheat genetic diversity (Sharma et al., 2015). However, employing morphological markers may be time-consuming and involve a significant trait-environment interaction. On the other side, wheat genetic diversity is better measured because to the emergence of technologies that detects polymorphism directly at the biochemical and molecular levels. As a result, study of genetic variety is best conducted at the protein and DNA levels, as DNA is the basic source of all biological information.

In addition, there have also been several initiatives to define wheat genetic diversity using biochemical markers. A comparison of protein profiles from unstressed and stressed organisms may lead to the discovery of proteins that are directly or indirectly involved in the stress response. Furthermore, the data more accurately reflects genetic diversity, as biochemical markers are direct results of gene expression (Huang et al., 2021). Among biochemical techniques, SDS-PAGE is widely used due to its simplicity and effectiveness for describing the genetic structure of germplasm (Sharma et al., 2015). Likewise, molecular markers have been frequently utilized to determine cultivar identification and purity, as well as to analyses genetic diversity in wheat. AS environmental influences have no effect on molecular markers, DNA can be extracted at any developmental stage (Abd El-Moneim et al., 2021). Overall, the use of molecular markers in wheat breeding programs has significantly increased the precision and efficiency of genetic research.

Furthermore, genetic diversity study of crop germplasm is an important step in breeding programs as it can aid in the selection of germplasms with greater diversity and better performance under specific conditions (Karakaya et al., 2022; Pour-Aboughadareh et al., 2017). Fundamental understanding of the genetic diversity of bread wheat (*Triticum aestivum* L.) is required for the development of improved varieties with superior features and greater resilience to environmental challenges. Numerous studies have been conducted to explore the genetic diversity of bread wheat using various molecular markers. Wang et al., (2014) conducted a genetic diversity study in a collection of global bread wheat germplasm using Diversity Arrays Technology (DArT) markers; they discovered significant genetic differences among wheat populations. The study emphasized the significance of protecting and harnessing various gene pools in order to unlock the genetic potential for wheat enhancement. Similarly, Akbari et al., (2006) used genotyping-by-sequencing (GBS) and genome-wide association study (GWAS) methodologies to investigate genetic diversity and discover loci linked with essential agronomic variables in bread wheat. Their findings provided insights into the genetic architecture of complex traits and laid the groundwork for marker-assisted breeding strategies. Furthermore, studies on genetic diversity have expanded to look at the links between landraces and current wheat varieties.

To evaluate genetic variation in a panel of landraces and elite bread wheat lines, Sehgal et al., (2017) used single nucleotide polymorphism (SNP) markers. The study discovered that these cultivars had low genetic diversity, underscoring the importance of adding genetic variation from landraces to improve the genetic diversity of bread wheat. Moreover, studies indicate that a narrow genetic base comes from domestication and existing breeding that have reduced genetic diversity in several species, including wheat (Badaeva et al., 2022). Polyploidization is another issue in which wheat is allohexaploid, formed by crosses involving three strongly linked diploid species; this limits genetic diversity of wheat. This strong linkage between these species limits the potential for new genetic combinations and variations in wheat populations (Dubcovsky and Dvorak, 2007). An additional argument is that the species is 10,000 years old, which is insufficient time for the species to accrue mutations or obtain alleles through natural or artificial interspecific cross-breeding

processes (El Baidouri et al., 2017). This argument suggests that the genetic diversity observed in wheat today is primarily a result of naturally occurring mutations and variations within the species itself. Furthermore, it highlights the limited opportunity for wheat to acquire genetic material from other species through cross-breeding, further supporting the notion that the genetic changes in wheat have occurred within its own gene pool over a relatively short period of time. This narrowing of wheat variability can have significant implications for global food security and agricultural sustainability. Additionally, the reduction in genetic variability has made wheat more susceptible to diseases and pests, as well as limiting its ability to adapt to changing environmental conditions (Salgotra and Chauhan, 2023). It also implies the urgent need for continued research and efforts to develop more resilient and adaptable wheat varieties that can withstand changing environmental conditions and meet the growing demand for this staple crop. To increase the genetic variety available for wheat breeding, several strategies, such as induced mutation, genetic transformation, and genome editing need to be used (Pour-Aboughadareh et al., 2021). Specifically, the utilization of these techniques can help in developing wheat varieties with improved yield potential, disease resistance, and nutritional quality. Likewise, genome editing can be a preferred method in future efforts to dissect and improve desired features for bread wheat, such as yield, disease resistance, and nutritional content. By precisely modifying specific genes, scientists can potentially enhance the overall quality and productivity of bread and wheat varieties, leading to more sustainable crops that can better meet the growing global demand for food. Molecular breeding tools such as genetic transformation, marker-assisted gene pyramiding, whole genome selection, and precision genome engineering can be used to incorporate functionally improved genes into a suitable varietal background, resulting in elite cultivars with high yield potential and desirable traits such as disease resistance.

2.5 Genetic diversity studies of bread wheat in Ethiopia

Exploration and characterization of genetic variation in bread wheat germplasm are critical steps towards identifying diverse and distinctive genetic resources for breeding operations. Numerous studies in Ethiopia have been conducted to investigate the genetic diversity of bread wheat using morphological markers (Karima et al., 2017; Belete et al., 2021; El-

Esawi et al., 2022), biochemical markers (Kuwabara, 2001; Morris et al., 2017; Tiruneh et al., 2015), and molecular markers (Ahmad et al., 2018; Asmamaw et al., 2019; Slim et al., 2019; Yang et al., 2020; Haque et al., 2021). Recent advances in molecular techniques have made it possible to employ DNA-based markers to estimate genetic variety. Several studies have used molecular markers such as microsatellites and single nucleotide polymorphisms (SNPs). Bread wheat genetic diversity research in Ethiopia has important significance for wheat breeding and conservation initiatives. By studying the genetic makeup of different varieties, traits can be identified that contribute to disease resistance, yield potential and nutritional quality. This knowledge can then be used to develop new wheat varieties that are better adapted to local conditions and have improved agronomic traits, ultimately benefiting farmers and food security in Ethiopia.

According to genetic diversity research in bread wheat, Ethiopia's germplasm contains a considerable wealth of genetic resources (Alemu et al., 2021). These genetic resources have the potential to aid in the production of better cultivars with higher yield, disease resistance, and environmental stress tolerance. The use of varied genetic materials in breeding programs can help to generate superior wheat varieties that answer specific challenges Ethiopian farmers confront. Hailu et al., (2005) used ISSR markers, and Belete et al., (2021) used SSR markers to analyze the diversity and population structure of Ethiopian bread wheat landraces. Their findings revealed significant genetic variation and population differentiation, with a potential to aid in the conservation and long-term utilization of Ethiopian wheat germplasm. Moreover, Kebede et al., (2017) reported, genetic diversity study on Ethiopian bread wheat accessions using SNP markers showed significant genetic diversity. This research, offer insights into the genetic makeup, helps to improve our knowledge of the variability and possible adaptation of Ethiopian bread wheat. Furthermore, these findings can help enhance breeding techniques for increasing yield, disease resistance, and overall quality of Ethiopian bread wheat types (Alemu et al., 2020).

2.6 Strip rust (*Puccinia striiformis* f. sp. tritici)

Stripe rust caused by the pathogen *Puccinia striiformis* Westend (Ps), which is classified in the kingdom of fungi under the class Urediniomycetes, order Uredinales, family Pucciniaceae, and genus *Puccinia*. *Puccinia striiformis* f.sp. tritici (Pst) requires an

obligatory parasite living in a host and biotrophs due to their technique of obtaining nutrients from living host cells to complete its life cycle (Khanfri et al., 2018). Because of these parasitic traits, most rust fungi are highly specialized diseases specific to certain host species. The pathogen identified as *Puccinia striiformis* f. sp. tritici, which most likely has originated in Southeast Asia, is a destructive fungal disease that poses a huge danger to global food security. Since its capacity to rapidly evolve and overcome resistance genes (Wellings, 2011; Ali et al., 2014). Stripe rust identified by the presence of yellow, straight-sided pustules in stripes on leaves and heads are thin and diverge in length (Figure 4 A). Moreover, yellow-orange spores are formed as the pustules mature, and as the condition advances, the tissues surrounding the pustules get brown and dry, giving them a burned look. One of the most recognizable features of stripe rust disease is the organization of pustules into stripes (Schirrmann et al., 2021). Stripe rust manifests itself as a swarm of yellow-to-orange urediniospores erupting from pustules grouped in elongated, thin stripes on leaves (Chen et al., 2014). On the other hand, stripe-rust-resistant wheat cultivars are defined by diverse infection types, ranging from no visible symptoms to little hypersensitive specks to uredinia surrounded by chlorosis or necrosis with restricted urediniospore development (Figure 4 A,B).



Figure 4. Stripe rust reactions in two wheat germplasm

2.6.1 Biology of the stripe rust

Yellow rust disease is known as stripe rust because adult plants have yellow stripes in the lines between their leaf veins, although when the infection is in seedlings, the urediniospores are in clusters (Figure 4) rather than stripes (Khanfri et al., 2018). Stripe rust affects a wide variety of cereal crops, mainly wheat (Mehmood et al., 2020), barley (Park et

al., 2023), and rye (Chen et al., 2014) (Table 1). Stripe rust biology has been intensively investigated in order to understand disease mechanisms and develop effective control techniques. The wind-borne urediniospores, the asexual spores responsible for infecting new host plants, chiefly aid in the spread of stripe rust. Since these spores can travel long distances, the disease can spread across regions and continents (Adrien et al., 2014; McTaggart et al., 2022). A variety of factors influence stripe rust intensity and prevalence, including environmental conditions and host vulnerability. The fungus prefers cool and damp environments and thrives in mild temperatures (Siham et al., 2018). However, stripe rust disease has recently become more severe in some warmer places than previously (Hovmiller et al., 2010; Chen et al., 2014). Furthermore, the susceptibility of host plants is important in disease progression, with different cultivars demonstrating variable levels of resistance. Stripe rust control is critical for limiting its influence on agricultural productivity. Producing resistant cultivars, crop rotation and timely sowing are two examples of integrated disease control measures that can help lower disease incidence (Krishna, 2023; Ma et al., 2009; Serpous et al., 2018).

Table 1. List of important sub-species of *P. striiformis* with their host specialization of plant

Sub-species	Host specialization	Example	Reference
<i>P. striiformis</i> f. sp. tritici	Wheat	<i>Triticum aestivum</i>	Zhao et al., 2013
<i>P. striiformis</i> f. sp. Hordei	Barley)	<i>Hordeum vulgare</i>	Chen et al., 2014
<i>P. striiformis</i> f. sp. Secalis	Rye	<i>Secale cereal</i>	Chen et al., 2014
<i>P. striiformis</i> f. sp. agropyron	Agropyron spp	<i>Agropyron cristatum</i>	Chen et al., 2014
<i>P. striiformis</i> f. sp. Elymi	Elymus spp.	<i>Elymus cylindricus</i>	Chen et al., 2014
<i>P. striiformis</i> f. sp. Dactylidis	Orchard grass	<i>Dactylis glomerata</i>	Huang, et al., 2019
<i>P. striiformis</i> f. sp. Poae	Blue grass	<i>Poa pratensis</i>	Jin and Hambleton, 2010

2.6.2 Life cycle of *Puccinia striiformis* f. sp. tritici

The life cycle of stripe rust is an important part of its biology. To complete its life cycle, *P. striiformis* f. sp. tritici requires two hosts called primary and alternate hosts. *P. striiformis* f. sp. tritici primary host is wheat, where it produces the deadly disease stripe rust (Chen et al., 2014). Most rust fungi that damage grasses and cereal crops have been studied for over

a century; however, an alternate host of *P. striiformis* f. sp. tritici remains elusive (Roelfs, 1992; Jin et al., 2010). Only the tell and uredinal phases of stripe rust were identified in the late nineteenth century, while the alternate host was searched among *Boraginaceae* species (Chen et al., 2014). In addition, the pathogen *P. striiformis* f. sp. tritici was recently detected in barberry species, which were recommended as alternate hosts, and sexual recombination was also shown to play a role in pathogen evolution (Jin et al., 2010). As a result, *P. striiformis* life cycle is completed on two taxonomically unrelated hosts in which *P. striiformis* f. sp. tritici produces five types of spores called urediniospores, teliospores, and basidiospores pycniospores and aeciospores (Figure 5). For asexual reproduction, it alternates between graminacea and barberry hosts (Jin et al., 2010). Since, host alternation is crucial for the survival and spread of *P. striiformis* in which it allows for genetic recombination and adaptation to different environments. During the reproductive cycle, haploid basidia infect the alternate host, barberry, causing haploid pycnia. Pycnia produces pycniospores, which spread and cross-fertilize with receptive hyphae to form the dikaryon, which consists of two unfused nuclei in each cell. The dikaryon goes through a sequence of mitotic cell divisions and differentiations before becoming basidia. These basidia then generate haploid, which serve as the fungus' principal mode of dissemination, allowing it to colonize new places and form new infections. Once these basidiospores find a suitable main host, they germinate and begin the infection process, completing the fungus's sexual cycle (Abebe, 2020). The hyphae spread through the barberry, creating dikaryotic aecia that disperse aeciospores.

The life cycle of stripe rust includes both dikaryotic uredial and telial stages, and the teliospores can generate haploid basidiospores (Chen, 2005). The pathogen survives the offseason on different hosts, such as barberry plants, where it develops urediniospores, which are specialized spores. When the spores drop on the plant's surface, they germinate and penetrate the leaf tissue, starting the infection process (Chen, 2000). Once inside the plant, the fungus multiplies and forms yellow-orange uredinia, which are powdery structures that carry additional spores. These spores can then be transferred by wind to infect surrounding plants, allowing the disease to spread quickly. Additionally, wheat leaf-infected teliospores are formed late in the growth season. These teliospores serve as the principal source of inoculum for the infection cycle the next year. They may survive harsh

winter circumstances, guaranteeing the pathogen's survival in the environment until favorable conditions for infection reappear (Figure 5). At the start of the growing season, diploid teliospores germinate on the host plant or even dead tissues. This produces haploid basidiospores, which are then disseminated by wind or other means (Leonard and Szabo, 2005). The basidiospores infect the alternative host via the stomatal cell walls, producing haploid spores, or pycnia, of various mating types. These haploid spores, subsequently fuse with spores of opposing mating types to generate dikaryotic mycelium. After that, the dikaryotic mycelium can colonize and proliferate within the alternative host, completing its life cycle. These aeciospores are then dispersed and can infect other host plants via wind or other mechanisms. When the aeciospores land on a suitable host, they germinate and begin the infection process (Kolmer et al., 2009). The dikaryotic aeciospores are dropped on the host plant, where they infect and colonize, subsequent in the development of urediniospores in which those urediniospores are primarily dikaryotic and asexual in nature. Urediniospores' asexual reproduction enables the rapid spread and colonization of new host plants. Under specific environmental conditions, dikaryotic urediniospores can undertake sexual recombination and teliospores are formed as a result. These teliospores are diploid and can withstand hard circumstances, allowing the fungus to live until better conditions emerge. Temperature, humidity, and nutrient availability all play a role in this process. Telia are essential for the survival of the fungus and spread because they produce basidiospores, which can infect additional host plants and complete the pathogen's life cycle (Julian et al., 2014).

The dikaryotic nature of the pathogene allows for genetic recombination, resulting in enhanced genetic diversity within the pathogen population. Furthermore, it promotes the emergence of new virulent races, which might represent a bigger danger to vulnerable plant species (Chan et al., 2014). This phase is to blame for the widespread stripe rust epidemics observed on cereal crops. As temperatures rise late in the epidemic phase, the pathogen produces thick-walled, mostly two-celled teliospores (Gultyaeva et al., 2022). Teliospores' thick walls also protect them from fungicides, making it difficult to control stripe rust outbreaks. The diploid nucleus of a mature teliospore undergoes karyogamy, a crucial step in the sexual reproduction of certain fungi, where the fusion of two haploid nuclei results in

the formation of a diploid nucleus (Mehmood et al., 2020). This fusion produces a genetically stable cell capable of going through meiosis and producing haploid spores for reproduction (Chenet et al., 2012). Moreover, *P. striiformis* was previously overlooked because it reproduces only asexually on wheat via dikaryotic uredospores, with teliospores produced at the conclusion of the cropping season unable to encounter an alternate host to complete the sexual cycle. Recent research indicates that *P. striiformis* can reproduce sexually on the alternative host, barberry, by creating basidiospores (Mehmood et al., 2020; Chen et al., 2021). This discovery has revealed new insights into the pathogen's life cycle and genetic diversity (Jin et al., 2010). The sexual cycle in uredinales involves the fusion of two different types of spores, resulting in genetic recombination and the production of new variations. This genetic diversity allows the fungus to adapt and survive during the offseason, when conditions may not be favorable for its asexual reproduction (de Vallavieille-Pope et al., 2012) (Figure 5).

The subsequent asexual cycle permits the fungi to spread continuously among wheat populations. The urediniospores produced by dikaryotic uredinia can reinfect wheat plants, resulting in the formation of new uredinia and the completion of the reproductive cycle (Hovmøller et al., 2011) (Figure 5). Subsequently, the asexual uredinial stage is important in contributing to the disease and sexual forms of the pathogene have rarely been observed. The rarity of observations of the pathogen's reproductive phases emphasizes the pathogen's dominance and impact (Milus et al., 2009; Wang and Chen, 2015). Furthered, there are several races of the pathogen, each with the ability to overcome specific resistance genes in cultivated crops. The pathogen-host plant co-evolutionary process is a continuing danger to agricultural output. To effectively control stripe rust, breeders have used genetic markers to identify and incorporate numerous resistance genes into commercial cultivars, thereby increasing their resistance to the disease. Still, stripe rust intensity and its impact on cereal crops are influenced by a number of factors. Temperature and humidity, for example, play a crucial role in disease development. High humidity and low temperatures (2-15 °C) promote disease growth and spread, although very high temperature can hinder it (Chen, 2020).

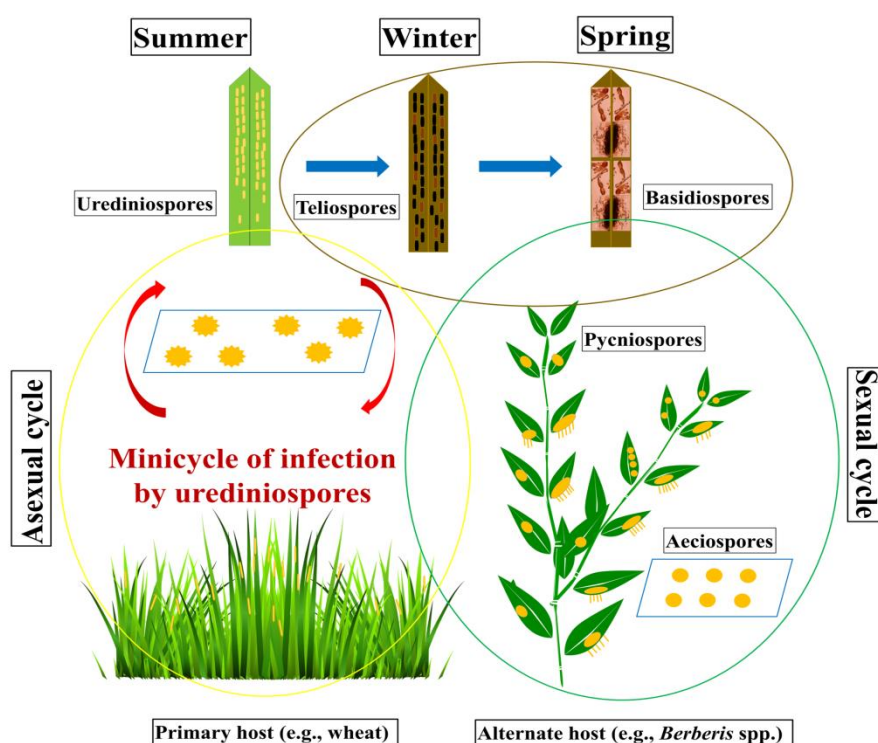


Figure 5. Life cycle for *Puccinia striiformis* (Source; Zhao et al., 2022)

2.6.3 Stripe rust diseases in Ethiopia

Rust diseases are the most economically important fungal pathogens that have been causing problems in cereal production for many years (Meyer et al., 2021). Stem, stripe and leaf rust disease, produced by a variety of fungus species, affects a wide range of crops and can result in major output losses and economic hardship for farmers all over the world (Meyer et al., 2021). Besides, stripe rust disease damages a wide range of economically essential crops, including wheat (Khondoker et al., 2021; Meyer et al., 2021), barley (Woldeab et al., 2007), coffee (Berihun and Alemu, 2022), which are critical to Ethiopia's economy. In addition, yellow rust disease has a significant influence on crop yield and infects foliage, causing typical rusty-colored lesions on leaves. These lesions diminish plants' photosynthetic capability (Rahmatov et al., 2015), affecting their ability to produce food and, in extreme cases, resulting in yield losses of up to 100% (Marsalis et al., 2006; Marsalis and Goldberg, 2016). As a result, rust disease weakened plants, which is manifested in poor quality of harvested produce, lowering market value and potentially limiting export options. Planting resistant wheat varieties, effective crop rotation, and

timely fungicide applications are all part of rust disease management measures (Akci, 2022). Regular rust population monitoring and early discovery are critical for effective control. Controlling prevalent fungal infections affecting wheat in Ethiopia necessitates a combination of techniques such as the use of resistant cultivars, crop rotation, timely fungicide applications, and good farm hygiene. Early detection, monitoring, and response are critical for disease control. Farmers may protect their wheat crops, maximize yields, and contribute to Ethiopia's overall food security and prosperity by implementing integrated disease management strategies (Carmona et al., 2020; Omara et al., 2022).

When it comes to treating rust disease, there are a number of obstacles in Ethiopia. These problems include a lack of availability of disease-resistant crop varieties, a lack of farmers' understanding of early diagnosis and effective control measures, and insufficient funds and resources for research and implementation of mitigation strategy (Bishaw et al., 2016; Allen-Sader et al., 2019). Furthermore, climate change and the advent of new rust races hamper efforts to effectively combat the disease. A multifaceted approach is required to reduce the effects of rust disease, this includes: breeding initiatives for crop resistance development and deployment should focus on generating rust-resistant crop varieties to provide farmers with disease-resistant options (Xu et al., 2013). Early identification and surveillance with monitoring systems, in conjunction with farmers, is critical for prompt detection and response to rust outbreaks. Interactively, agronomic approaches such as crop rotation, proper watering, and maintaining optimal plant nutrition are used to create an adverse environment for rust disease. To directly target and reduce the rust pathogen, fungicide treatments, which are environmentally desirable, can also be administered at key phases of crop growth when necessary (Martinez-Espinoza, 2008).

Stripe rust is a major threat to wheat production in Ethiopia, where agriculture is critical to the economy and livelihoods of millions. Stripe rust has emerged as one of Ethiopia's most damaging wheat diseases, causing significant crop losses and economic hardship for farmers (Meyer et al., 2021). The disease flourishes in chilly, moist environments, which are common in highland areas and during extended rainy seasons. Its propensity to spread quickly and infect wide wheat varieties amplifies its impact, making it a persistent source of concern for farmers across the country. In Ethiopia, yellow rust causes 36% to 100%

wheat crop loss (Ayele and Muche, 2019; Jaleta et al., 2019). Moreover, yellow rust was to blame for the failure of Ethiopia's dominant wheat varieties, including Dashen in 1994 (Ayele and Muche 2019) and Kubsu in 2010. These collapses resulted in considerable output losses and economic hardship for the region's farmers (Tadesse et al., 2018). Stripe rust epidemics occurred in all major wheat-growing areas of Ethiopia in 2010, resulting in significant output loss (Olivera-Firpo et al., 2015; Ayele and Muche, 2019; Hodson et al., 2020). This underscores the critical importance of developing and identifying novel stripe rust resistance genes in wheat in order to minimize future epidemics and guaranteeing the stability of Ethiopian wheat production. Efforts should be made to produce resistant cultivars that can withstand the threat of stripe rust and help farmers in the region reduce production losses.

Moreover, a key difficulty in Ethiopia is the shortage of effectively resistant wheat varieties. Since, *P. striiformis* has a high degree of genetic diversity, resulting in novel pathotypes that can defeat previously resistant genotypes (Villaréa et al., 2002; Duan et al., 2010; Gangwar et al., 2022). Most wheat varieties planted in the country are susceptible to stripe rust, exposing farmers to significant yield losses. The pathogen's continual evolution presents a considerable obstacle to efficiently nagging stripe rust. Lack of robust disease monitoring and early warning systems hinders effective management strategies. According to Ayele et al., (2008) investigations the previous two decades show that stripe rust has been widely spread in all bread wheat producing areas of Ethiopia practically, impacting nearly all improved varieties at several levels. The maximum level of stripe rust infection was seen in areas between 2150 and 2850 meters above sea level (Abebe 2020). Grain yield losses range from 30 to 96% on vulnerable bread wheat cultivars in Bale (Hailu and Fininsa, 2009), such as stripe rust, which reduced Dashen germination and kernel weight by 72% and 56%, respectively (Ayele and Wondimu, 1992).

Furthermore, monitoring hazardous pathogens and races, as well as inventorying the resistance genes used in wheat cultivars, are the most important aspects of a successful wheat breeding program. Breeders can indirectly assess the presence or absence of resistance genes in genotypes by discovering and evaluating these markers. This method is more efficient and accurate than standard phenotypic approaches for screening for

resistance because it eliminates the requirement for time-consuming and labor-intensive phenotypic assessments (Goutam et al., 2015). Furthermore, RAD, RFLP, SSR, and SNP markers are among the molecular markers associated with Yr genes (Zhou et al., 2014). However, progress in the development of related KASP-based SNP markers for the Yr genes has been slow, and there is still a need for more efficient and accurate marker-assisted selection methods in wheat breeding programs (Marchal et al., 2018). Kidane et al., (2017) reported the discovery of Yr genes with related genetic markers in Ethiopian durum wheat varieties; however, equivalent studies on durum wheat are sparse. When compared to SSRs and other PCR-based markers, KASP-based assays are known for their high-throughput capabilities and cost-effectiveness. Several germplasm evaluation initiatives for resistance to stripe rust are carried out in Ethiopia, employing phenotypic screening in the field and greenhouses. Together with the phenotyping method, the molecular screening strategy provides supplementary evidence for the reliable identification of resistance genes.

2.7 Stripe rust management methods

Since, stripe rust continues to be a major restriction on wheat output understanding the epidemiology of stripe rust can thus help to control it effectively (Merz and Falloon 2008). Urediniospores known to be aerielly dispersed are mostly close to the source, with considerable diffusion very far from the source lesion, in which modest amount of disease early in a growing season can lead to a serious epidemic (Farber et al., 2017). As, revealed by Zhao et al., (2016) urediniospores can move up to 800 kilometers. This long-distance dispersal makes stripe rust control difficult. On the other hand, development of resistant cultivars is one of the basic approaches to stripe rust management. A lot of progress was made in Ethiopia toward the development of resistant varieties, and numerous types with varying levels of stripe rust resistance were released for cultivation. However most of resistant varieties were less successful after their release, that was due to the entrance of exotic races or the emergence of new races and environmental effects (Wubishet and Chemed, 2015).

In addition, farmers' lack of awareness about the proper application of fungicides for this specific rust treatment may exacerbate the disease's high epidemics (Getachew, 2020; Meyer et al., 2017; Bhandari et al., 2019). Furthermore, Mengesha and Moral (2020) and

Yoon et al., (2013) showed that the repeated use of a single fungicide for multiple years resulted in the need for other broad-spectrum fungicides. These adverse effects include pollution of water supplies, harm to non-target organisms, and the development of fungicide resistance by the disease causing agents (Tesfaye et al., 2018). As a result, it is critical to examine alternative disease management strategies that minimize fungicide use and prioritize sustainable practices.

Since the cultivation of resistant cultivars is one of the key methods for controlling stripe rust, resistant cultivars with specific resistance genes have been generated effectively through breeding efforts (Hanson et al., 2016). Genes such as Yr10 (Din et al., 2023) and Yr15 (Kokhmetova et al., 2021) have been widely integrated into wheat cultivars to combat stripe rust (Zeng et al., 2014). These resistant genes considerably lower the severity and occurrence of the disease, allowing for long-term and sustainable management of stripe rust. Furthermore, cultural practices are important in the management of stripe rust; planting non-susceptible crops in the rotation can stop the disease cycle and decrease stripe rust population growth (Chen, 2005). Proper field cleaning such as removing infected agricultural debris also aids in limiting the fungus' spread and survival (Murray et al., 2005). Fungicide treatments are frequently utilized as an additional control tool, particularly when resistant cultivars are unavailable or vulnerable to new races of the disease. However, their long-term viability and resistance to development potential demand prudent and integrated use. As a result, an integrated approach including resistant cultivars, cultural methods, and careful fungicide application is advised for successful stripe rust management (Carmona et al., 2020). Regular field monitoring is critical for diagnosing the disease in its early stages and taking appropriate action (Drake et al., 2019). Collaborations between academics, breeders, and farmers are also critical for knowledge exchange and promoting the adoption of best management techniques.

2.7.1 Mechanisms of stripe rust resistance in wheat

Understanding the mechanisms underpinning stripe rust resistance is essential for breeding success. Resistance mechanisms have been identified that are both race-specific and non-race-specific (Vergara-Diaz et al., 2015). Besides, researchers are uncovering new insights into the complicated genetic relationships between wheat and stripe rust disease using

molecular approaches. Despite great advances in stripe rust resistant breeding, there are still obstacles. The pathogen's ever-changing nature (Wellings 2011) needs ongoing efforts to generate long-lasting resistance. Furthermore, the identification and inclusion of novel resistance genes, as well as the use of cutting-edge technology, show great promise for enhancing stripe rust resistance in wheat. Presence of particular stripe rust resistance genes (Yr) is one typical mechanism for resistance to stripe rust in wheat plants. These “Yr” genes identify certain pathogen avirulence genes (Avr) and initiate a defense response, eventually leading to stripe rust resistance. By 2019, 82 Yr genes had been permanently named (Huang et al., 2020) and several “Yr” genes such as Yr9 (Cheng et al., 2014) and Yr15 (Klymiuk et al., 2018), have been found and characterized as giving stripe rust resistance. These genes frequently encode proteins from the nucleotide-binding site leucine-rich repeat (NLR) family, which act as intracellular receptors to detect the presence of pathogens (Singh et al., 2015). The activation of defense-related signaling pathways is another significant mechanism of stripe rust resistance. Wheat plants activate various defense signaling pathways in response to pathogen detection, including the salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) pathways (Bai et al., 2023). These signaling pathways activate numerous defense-related genes, resulting in the generation of antibacterial chemicals, cell wall reinforcement, and hypersensitivity responses, all of which contribute to stripe rust resistance. Physical and chemical barriers, in addition to Yr genes and defense signaling pathways, play critical roles in stripe rust resistance (Lee et al., 2019). Fungal spore adherence and penetration can be hampered by wax coatings on leaf surfaces. Stripe rust resistance is also influenced by cuticle thickness and leaf stomatal density. Yield losses caused by the disease have ranged from 10-70% in several wheat producing locations, depending on the timing of the initial infection, cultivar susceptibility, disease duration, and rate of disease development (Chen, 2005). Strip rust-damaged crops generate seeds with low vigor and delayed emergence following germination. Stripe rust can cause up to 100% yield loss when infection occurs early in the growth season and infection develops throughout the growing season, assuming the cultivars are susceptible (Mahmoud et al., 2012; He et al., 2019).

Breeding for *P. staritiformis* resistance in Ethiopia is mostly based on field observations at naturally infected trial locations. This method is based on identifying plants that are resistant to *P. staritiformis* in the wild. Breeders can choose and disseminate promising resistance features by studying the performance of different types in naturally contaminated experimental areas. Besides, this strategy enables the assessment of how well resistant plants perform under a variety of environmental situations, offering useful information for future breeding efforts. Though, there is little information available on the genetic composition of current cultivars and even less on materials under selection (Dawit et al., 2012). Wheat genetic resources with linked parentage and a high prevalence of race-specific main gene resistance have served as the foundation of Ethiopian wheat development projects (Badebo, 2002). However, the majority of the released varieties in the country lack long-term resistance and became sensitive soon after they were released (Admassu et al., 2012). Additionally, regular monitoring and evaluation of pathogen populations can aid in the identification of new pathotypes as well as the timely updating of resistance gene deployment to keep up with emerging threats (Wubishet and Chemed, 2015). Adoption of slow-rusting cultivars can also contribute to sustainable agriculture by boosting long-term disease management measures (Tolassa et al., 2015). This aid in development of varieties that can tolerate changing races of yellow rust and reduce crop losses. Likewise, it is critical to work on diversifying resistance sources in order to ensure long-term disease effectiveness (Heiet al., 2015). It is critical to regularly monitor the pathogen's virulent races in order to stay up-to-date on their evolution and adaptability, ensuring that resistant genotypes remain effective in the long term.

2.7.2 Host plant resistance to yellow rust

Migration, mutation, and recombination have all contributed to the evolution of new virulence in rust-causing fungi. The continual arms race between the fungus and its host, as the host develops resistance mechanisms against the disease's virulence components drives this process. As a result, rust-causing fungi are continually changing and evolving to overcome host defenses (Bettgenhaeuser et al., 2014; Annan et al., 2023). There are two types of genetic resistance to yellow rust called qualitative and quantitative resistance. The qualitative resistance also called race-specific/vertical resistance/seedling resistance or

monogenic (main genes) resistance, while the quantitative resistance called non race specific/horizontal/ polygenic or minor genes resistance. The ability of a plant to totally inhibit the infection or growth of a certain race of stripe rust pathogen is referred to as qualitative resistance (Chen, 2005). Major genes that provide powerful and particular defensive mechanisms against the pathogen typically govern this sort of resistance. Quantitative resistance, on the other hand, involves numerous genes that collectively contribute to a plant's overall resistance against a wide range of yellow rust races in which this form of resistance is more common (Bouvet et al., 2022; Saeed et al., 2022).

2.7.2.1 Major gene resistance

Race-specific resistance is type of resistance that is common in crops, assisting them in combating specific pathogen-caused diseases. Gene-for-gene resistance is based on precise interactions between the host plant's genes and the pathogen's equivalent genes. When a new pathogen pathotype forms, it may have alternative genes that might avoid or surpass the host plant's defensive mechanism, rendering gene-for-gene resistance ineffective. As a result, ongoing monitoring and breeding for new resistant types are required to combat changing diseases (Knott 2008). Mundt (2014) defined a race-specific pathogen resistance that is relatively easily inherited. When the host plant's resistance gene identifies the pathogen's avirulence gene, it initiates a defense response that can impede or limit pathogen growth (Mapuranga et al., 2022). The gene-for-gene interaction model provides a framework for understanding how specific plant genes and pathogen genes interact to generate host-pathogen interaction outcomes (Mapuranga et al., 2022). This encounter sets off a chain reaction of defense responses in the plant, leading to resistance to the disease (Abebe, 2020).

Moreover, race-specific resistance works according to the gene-for-gene relationship; for every resistance gene in the host plant, there is an avirulence gene in the pathogen. It has been the subject of several breeding efforts involving quantitative trait loci (QTL) identification (Hou et al., 2015; Zhang, 2022), which can also be pyramided. According to Mapuranga et al., (2022), race-specific indicates that resistance to some infections has been acquired. Race-specific resistance is only effective against distinct races of a disease and is frequently based on genes that are active at the seedling stage and remain active throughout

the plant's life cycle. The majorities of yellow rust resistance genes are determined during seedling development and interact with specific races of the pathogen to impart resistance in a gene-for-gene interaction (Flor, 1971). Typically, race-specific resistance is mediated by a hypersensitive response governed by key genes (Mapuranga et al., 2022). As of their direct efficiency against specific races of diseases, the use of significant genes in cultivars has been a popular practice in the past. However, this technique alone might not be sustainable as infections rapidly evolve and overcome important gene resistances. As a result, researchers have changed their focus to building non-race-specific resistance mechanisms involving many genes, which will provide long-term protection against a broader range of infections.

2.7.2.2 Minor gene resistance

The genetic basis of nonrace-specific resistance is complex, relying on the additive interaction of a few or multiple genes with small to intermediate effects. These genes are in charge of numerous immunological responses and play an important part in determining a plant's ability to resist disease. Furthermore, environmental factors can impact the expression of these genes, adding to the intricacy of race-specific resistance. This form of resistance cannot be used to establish pathotypes, and it generally allows for a limited amount of rust sporulation (Cantila et al., 2020). However, the efficiency of this form of protection against different races of rust can vary. Furthermore, while it may slow the transmission of rust spores, it does not totally prevent their production or spread (Ellis et al., 2014). Minor gene resistance is most effective during the post-seedling and adult plant stages, as adult plant resistance (APR), which is frequently discovered in the field (Dinglasan et al., 2022). On the other hand, the majority of non-race-specific resistance testing was performed on adult plants (Ivanova et al., 2023). As a result, genes are thought to influence nonrace-specific resistance, leading to partial resistance and being linked to slow rusting resistance (Huerta-Espino et al., 2020).

To slow the spread of virulence, breeding programs necessitate the identification and application of collective resistance genes with small to intermediate effects (Singh et al., 2005). When the combined effects of yellow rust control compared to those of race-specific resistance gene, non-race-specific resistance provides genetic complexity, it is more

difficult for the pathogen to overcome than a single gene (Karelov et al., 2022). To tackle the newly developed yellow rust races, CIMMYT devised a technique of pyramiding minor genes alone or in combination with main genes (Rehman et al., 2013).

2.7.3 Wheat breeding for rust disease resistance

Fungicide control strategies may play an important role in an integrated disease management program. However, fungicides, which are used to prevent severe crop losses due to fungal disease, can, nevertheless, be a considerable variable expense in wheat production (Figueroa, 2018). In addition, fungicides have negative effects on human health and may lead to the spread of chemical-resistant pathogen races (Miedaner, 2013). As a result, increasing grain yield, resilience to biotic and abiotic stressors, and end-use and nutritional quality traits are among the most important breeding objectives in wheat improvement efforts around the world. In developing countries like Ethiopia it is concerning as wheat is primarily used for human consumption when population numbers continue to rise while land and water resources decline due to urbanization and unsustainable use. This leads to improved productivity through crop management and crop genetic improvement (Kayim et al., 2022). To meet wheat demand as the world population grows, agricultural supplies are expected to increase by 50% by 2050 (Braun et al., 2010). However, the biggest production pressures are biotic factors, such as disease pathogens, insects, pests, and weeds (Einar, 2007). These biotic factors have a negative impact on yield and grain quality (Bhavani et al., 2021). Fungal infections, particularly rust, have already caused large disease epidemics and continue to endanger wheat output, inflicting enormous and catastrophic crop loss (Kayim et al., 2022). To address these issues, wheat breeding programs around the world are incorporating rust resistance genes into commercial cultivars (Roland 2002; Gill et al., 2019), in which breeders can leverage genetic variability within adapted lines to select parents for hybrid formation in order to integrate the necessary genes. Plant breeding programs creating wheat cultivars are concerned about a limited genetic base of plant germplasm. Germplasm with wider genetic bases, on the other hand, can significantly enhance disease distribution in freshly released cultivars (Asif et al., 2005).

Yellow rust-resistant cultivars developed in the mid-1960s contained inherent resistance from an Indian variety called Anza, which had a high level of resistance and was released in countries such as South Sudan, South Africa, and New Zealand (Rehman et al., 2013). This long-lasting resistance was attributed to the presence of Yr18 gene, and it was widely utilized in spring and certain winter wheat types (Singh and Rajaram, 1992). In addition, Yr7 gene is also found in a variety of spring and winter wheat varieties, including Barani 83 (Yr7) and Pavon 76 (Yr6, Yr7, and Yr29) (Dubbin et al., 1989; Badebo et al., 1990) (Table2). Moreover, lines containing a translocation between rye 1R chromosomal segments and wheat chromosome segments were generated in the 1960s, and yellow rust resistance genes have been found on rye chromosome 1R's short arm (Riley and Macer, 1966). These genes were discovered to be linked to stem and leaf rust resistance genes, as well as cultivars called Salzmunder and Baertweizen, which had identical genes. Neuzutch, a sister line of those kinds, was utilized for breeding in the Soviet Union, giving rise to Russian cultivars including Kavkaz, Aurora, and many others (Rehman et al., 2013). Kavkaz and Aroua have an exchange chromosome with a 1B segment and a rye chromosome with a 1R segment, whereas Neuzutch has a complete 1R chromosome (Khan et al., 2013). As a result, Kavkaz was introduced into the CIMMYT germplasm as Veery, a high-yielding spring wheat cultivar.

Table 2. Some examples of yellow rust resistance genes in wheat varieties

Varieties	Resistant gene	Country	Year	Reference
Frontana	Yr 18	S. America	1943	Rehman et al., 2013
Lerma Rojo	Yra	Mexico	1964	McIntosh et al., 1995
Sonalika	Yr2 and YrA	India	1967	McIntosh et al., 1995
Bluebird	Yr6, YrA and Yr18	Mexico	1970	Singh et al., (1998)
Lyalpur 73	Yr 18	Pakistan	1973	Singh, (1992)
Pavon 76	Yr6, Yr7 and Yr29	Mexico	1976	Badebo et al., 1990
Ciano79	Yr 27	Mexico	1979	Rehman et al., 2013
Veery	Yr7 and Yr9	Globaly	1980	McIntosh et al., 1995
Barani 83	Yr7	Pakistan	1983	Dubbin et al., 1989

Further, wheat yellow rust's ever-changing nature poses a severe threat to future wheat output. A new, aggressive yellow rust race group has been causing major problems and has emerged as the dominant race in several nations (Ali et al., 2014). As a result, developing a yellow rust-resistant genotype is challenging (Kayim et al., 2022). As of the difficulty of

constantly shifting pathogen races, breeders advanced various kinds of yellow rust resistance with better longevity, such as gradual rusting or partial resistance (Singh et al., 2000). According to Bariana et al., (2001), durable yellow rust resistance is more likely to be adult plant type than seedling type and is not associated with the major genes responsible for hypersensitive reactions; rather, it is associated with minor genes known as yellow rust slow rusting genes (Rosewame et al., 2011; Rehman et al., 2013).

Wheat lines with transferred genetic material from related species, such as wheat-rye (Moskal et al., 2021), wheat-leymus (Feng et al., 2022), and wheat-thinopyrum (Guo et al., 2023) translocations or substitutions, are available. These wheat lines with transplanted genetic material from related species provide better genetic diversity as well as the possibility for improved attributes, including yellow rust disease resistance. The inclusion of genetic material from similar species results in wheat varieties increased wheat production sustainability. Those species are closely related to wheat and have significant traits that can improve disease and pest resistance, so breeders can incorporate these beneficial genes into wheat varieties, improving their overall performance and sustainability in agricultural systems. Furthermore, rye has been one of the most successfully exploited resources, helping wheat cope with biotic and abiotic stresses. Furthermore, genes *Yr8*, *Yr9*, *Yr15*, *Yr17*, *Yr24/26*, *Yr35*, *Yr36*, *Yr53*, *Yr64*, and *Yr65* (Shigang et al., 2017; Zeraf et al., 2020) were isolated from diploid and tetraploid wild and cultivated relatives of wheat, where *Yr15* originated from *Triticum dicoccoides* (Peng et al., 2000; Klymiuk et al., 2018), *Yr53* derived from *Triticum turgidum* (Liu et al., 2017). Additionally, *Yr37* from *Ae. kotschy* (Gideon et al., 2009; Ulaszewski et al., 2019), *Yr38* from *Ae. sharonensis* (Yu et al., 2022), *Yr40* from *Ae. geniculata* (Kuraparthi et al., 2007; Wang et al., 2021) and *Yr42* from *Ae. gengculata* (Marais et al., 2009; Kishii et al., 2019) have been used for stripe rust resistance to various races of the wheat and have generated encouraging results in breeding programs. Genes from hexaploid wheat landraces and wild relatives, *Yr5*, *Yr15*, *Yr53*, *Yr61*, *Yr65*, and *Yr69*, are still effective and can be employed in breeding for resistance to rust (Xu et al., 2013; Zhou et al., 2014).

2.8 Wheat genomics

The wheat genome has long been of interest due to its economic and agricultural importance. As a result, wheat genome sequencing marks significant advancement in scientific research. Furthermore, the wheat genome project has simplified the identification and characterization of genetic markers, which are critical tools in breeding programs. These markers help breeder's select desired traits quickly and precisely, reducing the time and resources needed to create improved wheat varieties. It also promotes food security and helps to meet the expanding global demand for this vital crop. Furthermore, wheat genomes are complex, with a high proportion of highly repetitive DNA (80-90% of the genome) (International Wheat Genome Sequencing Consortium, 2014), due to large genome sizes approximately (17 Gb for bread wheat; 12 Gb for durum wheat) (Gupta et al., 2008; Guan et al., 2020). The genome's vastness and complexity present constant hurdles, demanding ongoing advances in sequencing technologies and data analysis methodologies (Bush and Moore, 2012).

Collaborative efforts and continuous scientific investment are critical to unraveling the wheat genome's complexities and unleashing its full potential. Overall, the wheat genome project has been beneficial, providing vital insights into the genetic basis of wheat. It paves the way for further advancements in wheat agriculture, which will benefit farmers, consumers, and the global community as a whole. The situation has recently altered considerably, with the confluence of numerous technological advancements resulting in the production of new and more efficient resources that facilitate the establishment of comprehensive genomic programs in wheat (Feuillet and Muehlbauer, 2009). Innovative technologies and bioinformatics methods have also helped to solve these intricate genetic challenges. These new techniques helped in the knowledge of wheat evolution, domestication, and diversity, as well as in the improvement of agronomically essential wheat features (Feuillet and Muehlbauer, 2009). Furthermore, with the increased availability of genomic information for bread wheat and associated Triticeae species, wheat genetic and genomic research has been accelerated. This has significantly altered the way wheat agronomic qualities are examined and improved. Sunet et al., (2017) employed genome-wide association studies with plentiful molecular markers to successfully unveil

the genetic basis of complex characteristics. Using functional genomics methods, researchers can now effectively find gene expression related in the creation and variation of critical wheat features. Furthermore, multiplex editing allows for the destruction of large numbers of undesirable genes (or genetic components) as well as the simultaneous up-regulation of the functions of many genes controlling the same trait or process (Ma et al., 2015). Furthermore, by identifying essential genes responsible for desirable features, breeders can now create superior varieties with higher yields, disease resistance, and nutritional quality.

2.9 Quantitative trait loci mapping

Quantitative trait loci (QTL) mapping starts with bi-parental mapping, which includes the selection of parental lines with sufficient polymorphisms for the desired trait and susceptible parental lines for analysis; developing mapping populations, which can be backcross populations, F2 populations, or recombinant inbred lines (RIL). Next to parental selection, phenotyping of the mapping population for the target trait(s) is performed under appropriate conditions like greenhouses and/or open fields. Phenotyping involves carefully observing and recording the phenotypic variations exhibited by each individual in the mapping population. These observations help in identifying the individuals that possess the desired trait(s) and can be further utilized for genetic analysis and breeding purposes. Moreover, molecular profiling of the population requires an adequate number of uniformly spaced polymorphic markers to identify regions of the genome that are associated with the trait of interest. Then constructing a linkage map and identifying the QTLs underlying the target trait is done using suitable computer programs to analyze the genetic data and identify regions of the genome that are associated with the target trait. Once the QTL regions are identified, further analysis is conducted to validate and fine-map these regions, ultimately leading to the identification of candidate genes responsible for the trait. The linkage map serves as a foundation for comprehending the genetic links between various markers or genes in the genome. It enables scientists to estimate the relative placements of these markers and genes on the chromosomes, which is critical for understanding inheritance patterns and pinpointing regions of interest (Sehgal et al., 2016).

Some of the advantages of linkage mapping include: no population structure; relatively fewer markers for genome coverage; and the ability to locate QTL regions along chromosomes (Sorrells and Yu, 2009). Additionally, linkage mapping allows for the identification of genetic markers that are closely linked to the desired trait, making it easier to select individuals with desirable traits for breeding purposes. Linkage mapping studies have been critical in understanding the genetic basis of stripe rust resistance and finding candidate genes. Numerous studies have employed mapping populations to identify quantitative trait loci (QTLs) linked with stripe rust resistance (Rollar et al., 2021; Farzand et al., 2021; Brandt et al., 2021; Pang et al., 2022). To create high-density genetic maps, these investigations used a variety of molecular markers, including simple sequence repeats (SSRs) (Bokore et al., 2020; Eagle et al., 2022), single nucleotide polymorphisms (SNPs) (Zhou et al., 2022; Kumar et al., 2023), and diversity array technology (Singh et al., 2013; Jighly et al., 2015). The use of these markers aided in accurately identifying and mapping specific regions of the genome, allowing for a more comprehensive understanding of genetic variation within the population. Zhou et al., (2014) used an F2 populations resulting from a hybrid between two wheat cultivars with differing stripe rust resistance using SSR markers to create a linkage map and found numerous QTLs imparting resistance in various genomic regions.

Nowadays, the development and application of molecular marker technology have revolutionized the field of crop breeding by allowing breeders to select and manipulate specific genes with precision. It has also significantly accelerated the process of developing new varieties with improved traits, such as disease resistance. Molecular markers closely mapped to the desired gene or QTLs can serve as chromosomal landmarks to track the presence or introgression of the desired chromosomal region in breeding processes. Asad et al., (2012) and Yang et al., (2019) used the Infinium iSelect 90K wheat SNP array in one of their landmark experiments to study the genetic control of stripe rust resistance. They discovered numerous significant QTLs linked with stripe rust resistance in various wheat germplasm using a comprehensive QTL mapping approach. This work not only helped to understand the genetic pathways generating resistance, but it also suggested potential targets for marker-assisted breeding initiatives. Ye et al., (2019) used a genome-wide

association study (GWAS) approach to uncover QTLs for stripe rust resistance in wheat. This study was a significant step forward in understanding the genetic architecture of stripe rust resistance. Other notable QTL mapping studies have found major genes and QTLs that influence stripe rust resistance. Besides, Saintenac et al., (2018) uncovered the Yr15 resistance gene in durum wheat through mapping investigations. Similarly, Yang et al., (2019) used a RIL population obtained from a hybrid between two wheat cultivars to identify QTLs linked with stripe rust resistance. These QTL mapping studies add valuable information about the genetic regulation of stripe rust resistance.

2.10 Genome-wide association mapping

Genome-wide association mapping (GWAS) is an effective tool for identifying genetic variations linked to complex traits. It comprises screening an individual's or a population's complete genome for changes that are strongly related to a specific phenotype of interest (Visscher et al., 2012; Fan et al., 2016). GWAS is a promising method for dissecting genomic regions underpinning complex quantitative trait loci of interest in crops (Maccaferri et al., 2015). The process of performing a GWAS typically consists of many important components. The first stage is to identify representative study populations, which can include genotypes of various backgrounds with a substantial sample size and generate statistically meaningful results (Bush and Moore, 2012). Once the population has been determined, DNA samples are genotyped or sequenced to investigate millions of genetic markers across the genome. Genome arrays or next-generation sequencing technologies can be used in genotypic data, such as single-nucleotide polymorphisms (SNPs). The data acquired provide information on the genetic variants found in the population (Xiao et al., 2017). Following genotyping, quality control approaches can be used to eliminate markers with low call rates (Chen et al., 2016; Zhao et al., 2018), high messiness (Coleman et al., 2016), and minor allele frequencies (Coleman et al., 2016; Negro et al., 2019). Furthermore, population structure and relatedness analyses can be performed to account for relevant confounders of population stratification or familial relatedness (Hellwege et al., 2017). These steps serve to control for false-positive associations and improve the results' accuracy (Willer et al., 2010). Following the completion of quality control, association analyses are done to discover genetic variations linked to the phenotype under inquiry. To

analyze the connection between each genetic marker and the trait of interest, statistical tests can be used (Purcell et al., 2007). To account for the large number of markers evaluated concurrently, multiple testing correction methods, such as Bonferroni or false discovery rate, might be used following McCarthy (2008).

2.10.1 Phenotyping for genome-wide association mapping

The goal of GWAS is to find a link between genome-wide scanned SNP markers and a phenotype of interest that has been scored in a large number of genotypes (Korte and Farlow, 2013). The ability to precisely measure and describe phenotypic features is critical for identifying genetic variations linked to specific traits. In circumstances where polygenic characteristics with more complex genetic architectures are identified, increasing the sample size can improve the ability to recover meaningful marker-phenotype relationships (Louthan and Kay, 2011; Burghard et al., 2017). The identification and creation of standardized phenotypic methods is another key part of GWAS phenotyping. Standardization ensures that phenotypic measurements are similar across research, which makes data integration and comparison easier. For instance, using an incomplete block design (e.g., a lattice) in field design has the potential to boost mapping power (Piepho et al., 2006).

Accordingly, Messoadi et al., (2023) discovered stripe rust resistance in 200 elite spring bread wheat genotypes tested in a single area over two years with three replications per year. Similarly, Kokhmetova et al., (2021), discovered stripe rust resistance in 70 winter wheat genotypes in two locations and two seasons. Correspondingly, Vagndorf et al., (2018) investigated the genetic architecture of stripe rust resistance in 164 wheat genotypes tested over three years in three different locales. Additionally, Din et al., (2023) and Franco et al., (2022) used 93 lines and 245 bread wheat lines respectively, genotyped and tested at three locations for one year, to examine the genetic underpinnings of stripe rust resistance. All of this demonstrates that well-designed and repeated locations, as well as phenotype scoring in large sample sizes, are beneficial for detailed dissection of the genetic architecture of stripe rust resistance using GWAS approach.

2.10.2 Genotyping for genome-wide association mapping

Technological advances in genotyping have enabled the simultaneous analysis of millions of genetic markers. By identifying and addressing issues such as genotyping errors, missing data, and population stratification, quality control techniques assure the correctness and reliability of genotype data (Jiang et al., 2015). In GWAS, quality control entails a number of activities to identify and eliminate sources of error and bias. Moreover, duplicated samples are included in GWAS to verify genotyping consistency, which further ensures data accuracy (Lewis and Knight, 2012; Deelen et al., 2015). Genotypic differences between duplicates can help reveal genotyping errors or other sample management concerns. Additionally, platform-specific quality control filters can be used to account for potential biases produced by various genotyping technologies (Turner et al., 2011; Zeng et al., 2014; Peterson et al., 2019). In addition, in GWAS, imputation accuracy varies depending on reference panels and genotyping quality (Schurz et al., 2019; Zhang, Xiao et al., 2021). Thus, the core of GWAS is genotyping, which allows for the discovery of genetic variations across the genome. Besides, there are several genotyping systems available, including microarrays and next-generation sequencing methods. Microarrays give a low-cost, high-throughput option, whereas sequencing provides a more comprehensive picture of genetic variants (Bumgarner et al., 2013; Kwarteng et al., 2016). Besides, the genotyping platform chosen might be determined by the unique research objectives, budget, and sample size.

2.10.3 Genome-wide marker profiling in mapping populations

Genome-wide marker profiling in population mapping has transformed genetics by uncovering and examining genetic variants on an unprecedented scale. This method employs high-density markers distributed across the whole genome to build precise genetic maps that allow for accurate gene localization and trait mapping (Ganal et al., 2009). Genome-wide marker profiling is an effective approach for deciphering the genetic architecture underpinning complex characteristics. Researchers can construct high-resolution maps of genomic areas associated with certain traits or phenotypes using the capacity to test thousands to millions of genetic markers. This helps to understand the genetic basis of numerous features in crops, such as disease susceptibility. Moreover,

genome-wide marker profiling has transformed genetic mapping, allowing researchers to acquire significant insights into the discovery of genes and genetic variants linked to complex phenotypes (Kumar, 2012). As a result, choosing an appropriate genotyping platform is critical. A worthy SNP genotyping platform would be quick, robust, automatic, highly accurate, and inexpensive (Syvänen, 2001). It would also have the capability to process a large number of samples simultaneously, making it suitable for high-throughput applications. With the introduction of next-generation sequencing (NGS) technology, the time and cost of SNP genotyping have drastically decreased, increasing the usage of multiple SNPs (Kim et al., 2016). This technology enables the simultaneous analysis of a large number of SNPs, which provides a more comprehensive understanding of genetic variation within plant populations.

2.10.4 Techniques in genome-wide marker profiling

Single nucleotide polymorphism arrays (Qi et al., 2010), restriction site-associated DNA sequencing (MiMi et al., 2018), genotyping-by-sequencing (He et al., 2014), and whole genome sequencing (Bhattarai et al., 2021) are all used for genome-wide marker profiling. SNP arrays are frequently employed because of their ability to examine thousands of markers at the same time in an effective manner (You et al., 2018; Negro et al., 2019). Although restriction site-associated DNA sequencing and genotyping-by-sequencing approaches have lower marker densities, they are appropriate for non-model species with limited genetic resources. On the other hand, whole genome sequencing has the highest marker resolution and gives the most extensive genomic information, although at a higher expense. Moreover, genome-wide marker profiling for population mapping has a wide range of scientific applications. It facilitates the identification of quantitative trait loci responsible for significant agronomic features in plant genetics, allowing breeders to design improved crop varieties. It aids in understanding the genetic basis of traits related to disease resistance. Despite the numerous benefits of genome-wide marker profiling, there are several problems and limitations where data processing and interpretation can be difficult, necessitating the use of advanced bioinformatics tools and algorithms (O'Brien et al., 2012). Furthermore, data generation costs can be a constraint, particularly for large-scale investigations with varied mapping populations. The availability and quality of reference

genomes can also affect the mapping process's accuracy and resolution (Valiente-Mullor et al., 2021; Park et al., 2023). Genome-wide marker profiling will become more accessible and practicable for less funded projects and researchers as technology progresses. Besides, integrating genomic data with other omics technologies, such as transcriptomics and epigenomics can also provide a more complete understanding of gene regulation and trait variation.

2.10.4.1 SNP discovery through next generation sequencing

Since the early days of genomics research, the Sanger sequencing method has been used exclusively in DNA sequencing of various origins. Nevertheless, the low throughput and high genotyping cost of Sanger sequencing severely hampered its use in research. As a result, alternative sequencing methods that could offer higher throughput and cost-effectiveness were explored. One such method that emerged was next-generation sequencing (NGS), which revolutionized the field of genomics by enabling the simultaneous sequencing of millions of DNA fragments. NGS is faster and more cost-effective sequencing to analyze larger genomes and generate massive amounts of data in a shorter period of time. The first three commercially available NGS platforms are Roche 454 Genome Sequencer (Roche Diagnostics Corp.), Illumina Genome Analyzer (Illumina, Inc.), and SOLiD System (Life Technologies Corp.). These platforms have transformed the field of genomics by enabling high-throughput sequencing at a fraction of the cost and time compared to traditional Sanger sequencing methods.

The other group includes 'single-molecule' sequencing (SMS) technologies. These 'single molecule' sequencing technologies directly sequence individual DNA molecules without the need for PCR amplification. This eliminates the potential biases and errors introduced during the amplification process, making them advantageous for certain applications such as studying rare genetic variants or analyzing complex genomic regions (Makhoul et al., 2020; Shokralla et al., 2012). The identification of SNPs is critical for understanding genetic variants and their associations with diverse phenotypic features and diseases. Thanks to the introduction of NGS tools, the discipline of SNP discovery has advanced dramatically (Helyar et al., 2012). The findings from NGS-based SNP analysis have far-reaching ramifications. The discovery of SNPs has significantly improved our

understanding of population genetics, evolutionary biology, and disease genetics. It has aided in the discovery of genetic markers linked to complex traits, treatment responsiveness, and disease susceptibility.

Whole-genome sequencing covers the entire genome and is great for discovering rare and new SNPs. RRS and GBS approaches, on the other hand, allow for the focused sequencing of specified genomic areas, lowering sequencing costs while preserving SNP finding efficiency (Van Tassell et al., 2008). Since SNP identification is critical for downstream analyses, SNP calling algorithm advances in recent years have substantially increased the accuracy and efficiency of SNP detection (McKenna et al., 2010). Furthermore, machine learning algorithms have been progressively used for SNP calling, improving variation and detection accuracy. Whole-genome sequencing, for example, was utilized in a study by Li et al., (2009) to find millions of SNPs in several individuals, offering a rich resource for genetic variation analysis. On the other hand, Tennessen et al., (2012) used a focused sequencing technique, focusing on exonic areas in a large population cohort, to uncover rare functional variations associated with complex disease. These studies show the power of next-generation sequencing in SNP discovery and the implications for genetic research.

However, NGS is still vulnerable to high per-sample costs (Ishengoma et al., 2029; Kumar et al., 2022). These have necessitated the development of higher levels of sequencing, such as third and fourth-generation sequencing, which involve single DNA molecule sequencing without prior PCR amplification. Third-generation sequencing techniques like single-molecule real-time sequencing (SMRT) and nanopore sequencing have transformed genomics. These modern approaches provide extended read lengths, great accuracy, and the capacity to sequence DNA or RNA molecules directly without amplification. SMRT sequencing employs a DNA polymerase to incorporate fluorescently labeled nucleotides into a single DNA strand, whereas nanopore sequencing involves passing a DNA molecule through a nanopore and measuring electrical current changes as each nucleotide passes through (Srinivasan and Batra, 2014). Third-generation sequencing employs single-molecule templates rather than PCR amplification. This approach allows for the direct sequencing of DNA or RNA molecules without the need for amplification. Besides, third-generation sequencing offers advantages such as longer read lengths and the ability to

detect rare variants or modifications within a sample (Ku and Roukos, 2013). It is superior to prior sequencing platforms in that it requires less starting material, is faster, and has a lower error rate (Bleidorn et al., 2016). Additionally, the third-generation sequencing platform allows for simultaneous analysis of multiple samples in a shorter time frame, resulting in lengthy reads with average read lengths ranging from 5,000 to 15,000 bp (Lee et al., 2016). Furthermore, it provides more accurate and reliable results due to its advanced data processing algorithms and improved base-calling technology (Srinivasan and Batra, 2014). It was achieved through the use of advanced sequencing technologies such as PacBio and Oxford Nanopore, which have revolutionized genomics research by enabling the sequencing of large and complex genomes with higher accuracy and fewer assembly errors (Bleidorn et al., 2016). Similarly, third-generation sequencing technologies such as Illumina Tru-seq Synthetic Long-Read, have transformed genomics by allowing researchers to acquire longer reads and record more complicated genetic data. These sequencing technologies are especially effective for examining structural differences, gene expression patterns, and finding new genetic variants due to their capacity to produce lengthy reads (McCarthy et al., 2010; Hayan et al., 2021; Xiao and Zhou, 2020).

Massive parallel sequencing of nucleic acids directly within tissues or cells is the fourth-generation sequencing platform (Mignardi and Nilsson, 2014). This platform allows for the simultaneous analysis of multiple samples, providing high-throughput and cost-effective results. It has modernized the field of genomics by enabling researchers to study complex biological processes at an unprecedented level of detail (Hayan et al., 2016; Ke et al., 2016). On the other hand, the fourth-generation sequencing platform is nanopore sequencing technology. This technology utilizes nanopores, which are tiny holes in a membrane, to directly sequence DNA molecules. It offers several advantages over other sequencing methods, such as real-time sequencing and the ability to sequence long DNA fragments (up to 10,000 bp) (Lin et al., 2021). However, data processing and interpretation can be difficult, necessitating the use of sophisticated bioinformatics techniques and resources (Davey et al., 2011) and as the ever-increasing volume of genomic data presents storage and analysis issues (Al-Dous et al., 2011).

2.10.4.2 Genotyping by sequencing as SNP genotyping technology

Many studies have successfully used GBS in a variety of domains, including plant genetics, evolutionary biology, and conservation genomics. GBS has been used in species with large genome sizes, removing repetitive regions of the genome with restriction enzymes. Genome complexity reduction and sequencing only the lower copy regions of the genome makes NGS-based genotyping very simple, specific, quick, and vastly reproducible, while also confirming adequate overlap in the genome in sequence coverage (Elshir et al., 2011). This approach is particularly useful for studying complex genomes, such as those found in plants with large genomes by selectively targeting and sequencing the non-repetitive regions (Kumar et al., 2012). The relatively new and highly multiplexed GBS platform does SNP identification and genotyping at the same time and at a cheaper cost (Kim et al., 2016) and revolutionized plant breeding and genetic research by providing a cost-effective and efficient way to analyze genetic variations within a population (Bhattacharjee et al., 2020). Besides, the GBS platform made SNP identification, phylogenetic analysis, bi-parental mapping, candidate gene mapping, GWAS, and genome selection affordable to all plant researchers (Kumar et al., 2012). Also, GBS outperforms established genotyping technologies such as microarray-based SNP genotyping or targeted amplicon sequencing.

One of the most important advantages of GBS is its capacity to give genome-wide coverage, which allows for the detection of a huge number of SNPs across the entire genome. This thorough genotyping approach is especially useful for non-model organisms where genomic resources may be scarce. Furthermore, GBS is highly scalable technology that can genotype a large number of samples in a single experiment. Researchers can obtain high throughput by multiplexing samples, saving both time and cost when compared to conventional genotyping approaches. Furthermore, GBS facilitates the study of genetic diversity and population organization by allowing the discovery of novel genetic variants (Elshir et al., 2011).

2.10.4.3 Linkage disequilibrium estimation in wheat

Several recombination events can occur during meiosis, and hence, only closely located alleles can be co-inherited. Such non-random co-segregation of alleles at nearby loci is

called linkage disequilibrium (LD) (Xu, 2010). LD is an important concept in population genetics as it provides insights into the evolutionary history and genetic structure of populations. It can be used to identify regions of the genome that are under selection or have undergone recent changes. Additionally, LD patterns can be utilized in genome-wide association studies to identify genetic variants associated with complex traits such as diseases (Burghard et al., 2017). In numerous organisms, including wheat, linkage disequilibrium assessment is critical for understanding population genetic structure and selecting acceptable genetic markers. Accurate assessment of LD in wheat populations is critical for a variety of scientific applications, including genome-wide association studies, marker-assisted breeding, and genetic diversity study.

Several approaches for measuring LD in wheat have been developed, utilizing various types of genetic markers such as single nucleotide polymorphisms (SNPs) (Nimmakayala et al., 2014), simple sequence repeats (SSRs) (Daryl et al., 2007; Wang et al., 2013), and diversity array technology (DArT) (O'Connor et al., 2019) markers. These developments allow for more exact LD estimation as well as the finding of novel LD patterns related with important agronomic variables. Furthermore, estimating linkage disequilibrium is critical in genome-wide association studies and genomic selection in wheat (Zhao, et al., 2007). Significant progress has been achieved in the development and implementation of LD estimation methods in wheat in recent years. The calculation of Pearson's correlation coefficient, which evaluates the degree of relationship between allele frequencies at distinct loci, is one method. The other LD measurement method called r^2 , which evaluates the amount of non-random allelic association between loci, is extensively used in linkage disequilibrium estimation approach. This approach has gained popularity since it can detect both strong and weak LD signals (Gupta, 2005). Furthermore, r^2 accounts for changes in allele frequency among populations, making it valuable for researching varied wheat germplasm. Haplotype-based linkage disequilibrium estimation is a more advanced approach that takes into account the simultaneous occurrence of many loci in linkage disequilibrium analysis (Alemu et al., 2022). This strategy improves comprehension of linkage disequilibrium patterns within genomic areas, making it easier to identify haplotype blocks linked with complicated features (Difabachew et al., 2023).

Furthermore, as high-throughput genotyping technologies have become available, linkage disequilibrium estimate approaches have been integrated into powerful software packages such as TASSEL (Dadshani et al., 2021; Roncallo et al., 2021) and Genomic Association and Prediction Integrated Tool (GAPIT) (Mathew et al., 2019; Srungarapu et al., 2022; Peng et al., 2022). These tools provide user-friendly interfaces and quick algorithms, allowing researchers to estimate LD reliably and swiftly perform downstream studies. To summarize, accurately estimating LD in wheat is critical for understanding the genetic architecture underpinning key agronomic aspects.

As a fundamental concept in population genetics, linkage disequilibrium appears in a wide range of contexts, including association mapping and natural selection detection (Kang et al., 2019). All linkage disequilibrium statistics measure the difference between the observed and expected haplotype frequencies (Mackay and Powell, 2007). LD statistics are commonly used in population genetics to study the extent of LD between genetic markers and provide valuable insights into the genetic structure and evolutionary history of populations. The concept of r^2 is commonly used in population genetics and genetic association studies to measure the extent of linkage disequilibrium between two genetic loci. It provides insights into the patterns of genetic variation and can help identify regions of the genome that may be under selection or associated with certain traits, such as diseases. The value of r^2 ranges from 0 to 1, where $r^2 = 0$ implies the two loci are inherited independently, and the value of r^2 near 1 indicates the frequencies of co-segregation of alleles at two loci are higher (Slatkin, 2008).

Since r^2 is less sensitive to small sample sizes and low allele frequencies (Martinez et al., 2006), it is better at identifying how markers may be linked to QTLs of interest. As a result, researchers prefer the r^2 statistics over other alternatives of linkage disequilibrium, such as LD prime (D'). Moreover, the r^2 statistics provides a more accurate representation of the strength of LD between markers and QTLs, allowing researchers to make more reliable inferences (Sun et al., 2016). Additionally, the r^2 statistics can help identify rare variants that may have significant effects on phenotypic traits (Momozawa et al., 2021). For LD estimation, more advanced techniques, such as maximum likelihood methods, are also available (Gomez-Raya, 2012; Feder et al., 2012). These techniques take into account the

complex relationships between LD patterns and can provide more accurate estimates. Additionally, they can handle larger datasets and incorporate additional factors such as population structure or genetic admixture (Otyama et al., 2019).

In addition to TASSEL (Bradbury et al., 2007) and GAPIT (Zhiwu Zhang Lab, 2020), other freely available software tools can be used to determine the degree and pattern of LD, including Powermarker (Liu and Muse, 2005). These software tools utilize various statistical methods and algorithms to analyze the genetic data, detect the presence of LD, and offer a convenient and efficient way to explore the relationship between genetic markers and identify potential associations or patterns.

2.10.4.4 Decay in wheat

The extent of linkage disequilibrium in wheat varies with sub-genomes and chromosomes and is influenced by factors such as recombination rate, allele frequency, genetic drift, population structure, natural selection, and chromosomal rearrangements (Habib et al., 2020). Further, the r^2 plots provide valuable insights into the LD patterns and the extent of genetic recombination between alleles. They can help identify regions of high LD, which may indicate the presence of functional variants or genetic changes. Additionally, LD decay plots can be used to estimate the effective population size and historical recombination rates within a population. Moreover, plotting the r^2 values for all pairs-wise allele combinations against the genetic or physical distance between the alleles at the chromosome or at the entire genome level to generate linkage disequilibrium decay plots or disequilibrium matrices is likely (Laid et al., 2014; Roncallo et al., 2021). For a single chromosome or the complete genome, the graph displays the rate at which linkage disequilibrium drops with distance (Gupta et al., 2005). This curve is commonly used to model the decay of luminescence signals over time. It takes into account various factors, such as the initial signal strength and the rate of decay. The Loess fitting curve provides a more accurate representation of linkage disequilibrium decay (Habtemariam et al., 2014). Besides, linkage disequilibrium decay is commonly used to measure the extent of LD within a population and provides insights into genetic relatedness and evolutionary processes. The average LD decay of a population is thought to be the point when the Loesse curve intersects the $r^2 = 0.1$ threshold (Pasam et al., 2012). The cutoff value ensures

that only strong associations between variables are considered in the calculations. It helps to filter out weaker correlations that may not be reliable or meaningful for analysis. The cutoff value for association between all pairs of variables is $r^2 = 0.2$ for more trustworthy calculations.

Wheat linkage disequilibrium pattern and strength differed across chromosomes and genomes. These differences suggest that the genetic control of linkage disequilibrium varies between different regions of the wheat genome. Understanding these variations could provide valuable insights into the evolutionary history and breeding potential of wheat varieties. According to Hussain et al., (2022), the intra-chromosome linkage disequilibrium of Pakistani spring wheat accessions linkage disequilibrium decays at 0.34 Mbp for the whole genome and 0.29 Mbp, 0.2 Mbp, and 0.07 Mbp for all subgenomes A, B, and D, respectively. Among the three genomes, the B genome had the highest proportion of significant linkage disequilibrium (Chen, Min et al., 2012; Rabieyan et al., 2023). Similarly, Li, et al., (2019) reported the lowest linkage disequilibrium decay value at the D genome, such as 0.35, 0.75, and 0.25 Mb at the A, B, and D subgenomes, respectively. Kidane et al., (2021) also discovered that the LD between all SNP marker pairings in 300 Ethiopian durum wheat genotypes was less than $r^2 = 0.2$. Since there are substantial discrepancies in study population size, linkage disequilibrium significance threshold (r^2) value, and marker type, it is difficult to draw broad conclusions regarding LD patterns and trends in wheat. Each association panel should most likely be subjected to chromosomal and genome-wide linkage disequilibrium analyses.

2.10.5 Controlling population structure in genome-wide association studies

Genome-wide association studies (GWAS) have revolutionized our understanding of the genetic basis of complex traits, including diseases. However, accounting for population structure is one of the most difficult components of GWAS, which can lead to spurious associations and lower power. Numerous ways for controlling and correcting population structure in GWAS analysis have been developed to address these challenges. Principal component analysis (PCA) is a popular method for identifying important sources of genetic variation and incorporating them as variables into statistical models. By using PCA-derived main components as variables, population stratification can be controlled, resulting in more

accurate findings. This method has been widely used in GWAS studies and has shown exceptional success in minimizing false-positive linkages by population structure (Price et al., 2006).

Recently, the PCA has been considered a quick and effective method of managing population structure (Zhu and Yu, 2009). PCA reduces the dimensionality of a dataset while retaining most of its variability and can identify the major sources of variation in a population and account for them in subsequent analyses (Elhaik et al., 2022). The Bayesian information criterion can be used to estimate the optimal number of PCs and variables to include in the GWAS model. The Bayesian information criterion (BIC) is a statistical measure that balances the goodness of fit of a model with its complexity. In the context of GWAS, BIC can help determine the most appropriate number of principal components (PCs) and variables to include in the model. By penalizing overly complex models, BIC provides a quantitative approach to selecting the optimal combination of PCs and variables that maximizes model performance while minimizing overfitting (Zhiwu Zhang Lab, 2020). Since Bayesian information criteria help in determining the most relevant variables and PCs that contribute significantly to the model's predictive power (Bartoniczek et al., 2021). These statistical models help in accounting for confounding factors and controlling for potential biases that may arise from population stratification or familial relatedness (Hoffman et al., 2013; Taotao and Elizabeth, 2023). By incorporating Q-matrix, PCA, and kinship matrix information, researchers can obtain more accurate and reliable results, leading to a better understanding of the associations being studied.

Conducting structured associations (SA) is one of numerous strategies used to adjust for the effect of population structure (Pritchard et al., 2000). SA involves grouping individuals based on genetic similarity and then analyzing the association between genetic variants and traits within each group by searching a population for strongly related clusters using a Bayesian model-based algorithm, and then using the clustering matrices (Q) as covariates in association analysis (Sehgal et al., 2016). This approach allows for the identification of genetic variants that are associated with specific clusters within the population, providing insights into potential subpopulations or genetic substructures. By incorporating the clustering matrices as covariates, the method accounts for the underlying population

structure and improve the accuracy of association analysis. Using multiple models, the STRUCTURE program (Pritchard et al., 2000) can estimate population structure and kinship (shared co-ancestry coefficients) between individuals of population subdivisions. In which, structure software is widely used in population genetics that employs Bayesian inference to estimate the number of populations and individual ancestry proportions. It utilizes genetic marker data to infer population structure and can also estimate the degree of relatedness between individuals within populations (Porras-Hurtado et al., 2013).

2.10.6 Statistical models for genome-wide association studies

Several GWAS statistical models are widely used in genetic studies to analyze the relationship between genetic variants and phenotypic traits (Yu et al., 2006). The widely used methods are:

General linear models (GLM): The general linear model reduces false-positive connections by using the population structure matrix (Q-matrix) to account for population structure. This matrix allows distinguishing between true genetic associations and those that are simply due to population stratification (Yang et al., 2016).

Mixed linear models (MLM): MLM contains the kinship (K) matrix; it allows incorporating the familial relatedness among individuals into their analysis, providing a more accurate understanding of the data. By including the K matrix alongside the Q matrix, better account for genetic and environmental factors that may influence the observed outcomes (Pritchard et al., 2000). The "Q+K" approach is especially beneficial in complicated trait studies since it provides for a better understanding of the underlying genetic components that contribute to the trait. Furthermore, when compared to techniques that solely evaluate population structure or relatedness, the "Q+K" strategy has been demonstrated to minimize false positive correlations and enhance statistical power. This combined approach is particularly useful in studies involving complex traits.

Compressed MLM (CMLM): CMLM is an approach that addresses the confounding issue of MLM by utilizing cluster analysis to group individuals with similar characteristics (Kaler et al., 2019; Zhiwu Zhang Lab, 2020) by incorporating the elements of the kinship matrix as

similarity measures. CMLM enhances the accuracy and reliability of the clustering analysis, leading to more robust results. To group, several linking criteria (e.g., unweighted pair group method with arithmetic mean, UPGMA) can be utilized. These linkage criteria are based on different mathematical algorithms that calculate the distance and determine their similarity. The user can choose the number of groups based on their specific requirements or analysis goals. Once the lines have been classified, summary statistics of kinship between and within groups are utilized to construct a reduced kinship matrix. CMLM can give insights into the overall genetic relatedness and structure of the population. These reduced matrices are crucial in studying various genetic phenomena and making comparisons across different compression levels.

Enriched MLM (ECMLM): ECMLM enables more effective genetic data analysis by lowering the dimensionality of the issue and exploiting common genetic information within groups. This method not only expedites the analysis but also increases the accuracy of genetic predictions. ECMLM helps researchers find patterns and linkages that may have been ignored in standard analysis by efficiently grouping comparable genomic material together. Furthermore, this strategy can aid in the discovery of new insights and potential genetic markers linked to particular traits (Li et al., 2014).

MLM settlement under progressively exclusive relationships (SUPER): SUPER employs kinship derived from linked markers to mitigate the perplexing influence of familial relatedness (Wang et al., 2014). By utilizing linked markers, SUPER is able to distinguish between individuals who may share familial relatedness but have different genetic characteristics. This enables more accurate analysis and interpretation by decreasing the possibility of misinterpretation created by familial relationships (Wang et al., 2022). SUPER allows effective control of the effects of population stratification and relatedness, ensuring that the analysis focuses solely on the markers of interest. By excluding markers in strong linkage disequilibrium, SUPER minimizes the potential bias caused by these markers and provides more accurate results.

Fixed and random model circulating probability unification (FarmCPU): FarmCPU was created to address the issue of false positive control and confounding between testing

markers and cofactors at the same time (Liu et al., 2016). FarmCPU is a statistical method that effectively addresses the issue of spurious associations caused by population structure and relatedness in genome-wide association studies. By incorporating both marker and cofactor information, FarmCPU provides a robust framework for the accurate identification of true genetic associations. This approach has proven to be particularly useful in plant breeding programs, where controlling for confounding factors is crucial for selecting superior genotypes. It iteratively employs both the fixed effect model and the random effect model.

The fixed effect model assumes that the effects of all variables are constant across different observations, while the random effect model allows for variation in these effects. By applying both models iteratively, it helps to determine which model provides a better fit for the data and allows for more robust statistical analysis. The fixed effect model takes into account variance produced by particular factors, such as genotype, whereas the random effect model takes into account variation caused by unobserved factors. The fixed effect model posits that certain factors remain constant across all observations, allowing for direct comparison. The random effect model, on the other hand, recognizes that unseen factors might fluctuate between data, generating uncertainty in the measurement of their effects. By applying both models iteratively, FarmCPU effectively captures and accounts for various sources of variation in the data (Liu et al., 2016). The associated markers detected during iterations are fitted as cofactors to control false positives when testing the remaining markers in a fixed effect model. This approach helps to minimize the chances of incorrectly identifying markers as significant when they are actually not. By using the associated markers as cofactors, the fixed effect model can provide more accurate results in identifying truly significant markers. To avoid the overfitting problem in stepwise regression, a random effect model is used to select the associated markers using the maximum likelihood method (Liu et al., 2014).

The random effect model takes into account the correlation between markers and adjusts for potential confounding factors, resulting in a more robust and reliable selection process. Because FarmCPU examines markers in a fixed effect model, it is more computationally efficient than techniques that test markers in a random effect model, such as ECMLM and

SUPER. FarmCPU minimizes the requirement to estimate variance components for each marker in a fixed effect model, reducing computing overhead. Furthermore, the fixed effect model provides for greater control of confounding variables, resulting in more accurate results (Liu et al., 2016). This computational efficiency of FarmCPU is particularly advantageous when analyzing large-scale datasets with numerous markers.

Bayesian information and linkage-disequilibrium iteratively nested keyways (BLINK): BLINK was created with the goal of being both statistically powerful and computationally efficient. BLINK can analyze enormous datasets with amazing speed and precision by leveraging innovative algorithms and parallel processing techniques. Its strong statistical foundation provides dependable results, making it a vital tool for researchers and data scientists across the board (Huang et al., 2019). It incorporates advanced algorithms and techniques to ensure accurate and rapid analysis of data. BLINK increased computational speed and statistical power by comparing the maximum likelihood of a random effect model to the Bayesian information content of a fixed effect model using linkage distribution. This method allows for a more efficient and precise parameter estimate, resulting in faster and more dependable outcomes. BLINK not only enhances computational efficiency but also ensures more robust and reliable results, making BLINK a valuable tool in various fields such as genetics and population studies (Zhiwu Zhang Lab, 2020). Furthermore, BLINK's incorporation of linkage disequilibrium information helped in capturing the underlying genetic structure and minimizing potential confounding factors in the data (Muktar et al., 2022) (Figure 6). It was inspired to achieve two significant changes; the first change is to remove the FarmCPU-required assumption that causative genes are uniformly distributed across the genome. This assumption can lead to inaccurate results and hinder the identification of true causal genes. By removing this assumption, FarmCPU can more accurately identify the specific genomic regions where causal genes are located, improving the overall accuracy and reliability of the analysis. BLINK operates on markers rather than bins. Markers in linkage disequilibrium with the only most important marker are included. This approach ensures that BLINK focuses on the most informative markers for association analysis. By excluding markers in linkage disequilibrium with the most significant marker, BLINK reduces redundancy and prevents overrepresentation of correlated markers in the analysis. This

stepwise exclusion process allows for a more precise identification of independent markers associated with the trait of interest. Another modification is to use the Bayesian Information Content (BIC) of a fixed effect model to approximate the maximum likelihood of a random effect model in order to select the associated markers among those that remain excluded based on linkage disequilibrium. This approach allows for a more efficient and accurate selection of markers, as it takes into account both the likelihood of the model and the complexity of the marker. By incorporating BIC, can better assess the trade-off between model fit and model complexity, resulting in a more robust marker selection process. Using the BLINK C version, a dataset containing one million markers can be solved in hours (Huang et al., 2019). The BLINK R version can be run as standard or via GAPIT.

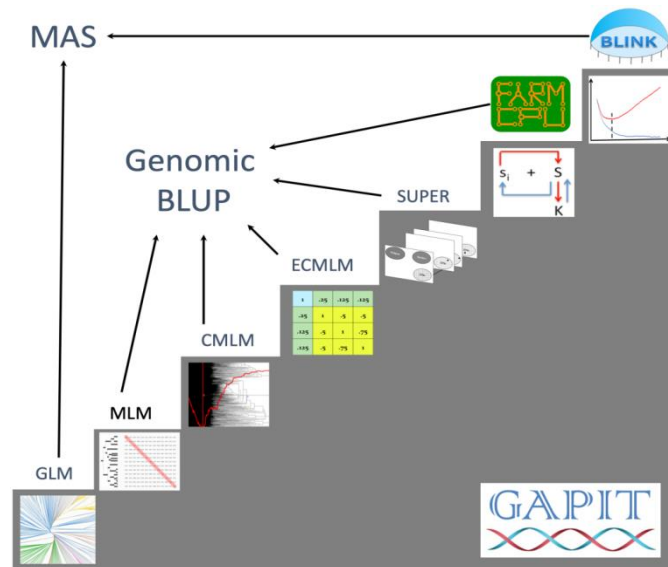


Figure 6. GAPIT-implemented GWAS (source; Huang, et al., 2019), All the methods support GWAS, including GLM, MLM, CMLM, ECMLM, SUPER, FarmCPU and BLINK

These models provide a framework for assessing the significance of genetic associations and controlling for confounding factors (Zhiwu Zhang Lab, 2020). Wheat has been discovered to have several levels of population structure. Soumya et al., (2021), identified three subpopulations in 82 bread wheat accessions tested for population structure using 35 K Wheat Breeder's Affymetrix array. Similarly, Mulugeta et al., (2023) identified five subpopulations in a population structure study of a 46 durum wheat landraces panel from Ethiopia genotyped with 25k wheat single nucleotide polymorphism (SNP) array. Moreover, Mahboubi et al., (2020) used DArT-seq platform to identify four subpopulations

in 129 Iranian wheat genotypes. Hashem et al., (2023) also revealed two subpopulations in a population structure analysis of 138 highly diverse spring wheat accessions genotyped with DArT markers.

2.10.7 Software Programs for genome-wide association studies

In response to advances in sequencing and genotyping technologies, several software applications have been developed to efficiently use sequence information. These software applications enable the analysis of large-scale genomic data and the identification of specific genetic variations that are associated with complex traits. By understanding the genetic architecture of these traits, scientists can make more informed decisions in crop improvement programs, leading to the development of improved and resilient crop varieties. Some of the commonly used software tools for genomic analysis and association studies are TASSEL (Bradbury et al., 2007), GAPIT (Zhiwu Zhang Lab, 2020), and the KD Compute PlugIn system. These tools provide a wide range of functionalities, such as data preprocessing, statistical analysis, and visualization, to facilitate the exploration and interpretation of genomic data. Additionally, they often offer user-friendly interfaces and comprehensive documentation to support researchers in their analyses (Bradbury et al., 2007). For example, TASSEL is used for the imputation of missing data, LD analysis, and data visualization (Sehga et al., 2016). TASSEL, created by Bradbury et al., in 2007, is a comprehensive and user-friendly GWAS software tool. It includes a comprehensive set of tools for data quality management, statistical analysis, and visualization. TASSEL supports a variety of marker types and can efficiently handle large-scale genomic datasets. TASSEL has also been widely used in genome-wide association studies (GWAS) to identify genetic variants associated with complex traits and diseases (Bradbury et al., 2007; Zhang et al., 2010). It provides researchers with a comprehensive suite of tools for analyzing large-scale genomic data and making informed decisions in plant and animal breeding programs. For example, TASSEL 5.0 incorporates CMLM for processing large data sets containing up to 500,000 markers (Sehga et al., 2016).

Another sophisticated software tool extensively used in GWAS is GAPIT. GAPIT, which was created by Lipka et al., in 2012, offers a set of advanced GWAS capabilities such as marker-trait association analysis, genomic prediction, and high-dimensional visualization.

It uses cutting-edge statistical methods and machine learning approaches to decipher the intricate links between genetics and phenotype. TASSEL's comprehensive support for numerous marker types is one of its main characteristics, making it suited for many genotyping systems. It also includes a number of statistical models for controlling for population structure and relatedness, which improves the accuracy of association analysis. GAPIT, on the other hand, stands out for emphasizing the use of sophisticated statistical approaches, such as BLINK, to account for complicated genetic architectures and population structure effects. The incorporation of genomic prediction capabilities enables the evaluation of marker predictive power, assists in the identification of potential candidates for breeding operations, and improves selection efficiency. Furthermore, GAPIT offers a user-friendly interface for conducting comprehensive genome-wide association studies and making predictions for genomic selection. GAPIT is also an innovative and simple-to-use R package utility that incorporates GLM, MLM, CMLM, ECMLM, SUPER, FarmCPU, and BLINK, often used for genome-wide association research as well as genomic selection and prediction (Lipka et al., 2012; Zhiwu Zhang Lab, 2020). These cutting-edge computing methods, such as BLINK, are specifically designed to handle large-scale genomic data and provide accurate predictions for various genetic traits. The package also offers user-friendly interfaces and comprehensive documentation to facilitate easy implementation and interpretation of the results (Lipka et al., 2012). Another prominent software system for association mapping is the KDCompute Plug-in System, which is a web-based analysis platform that is based on secure, customizable, and collaborative plugin architecture (DART, 2019). This platform allows users to perform complex computations and data analysis tasks efficiently. It offers a wide range of features and tools that can be tailored to meet the specific needs of different studies. With its secure infrastructure, users can confidently work on sensitive data while collaborating with team members in real-time.

2.10.8 Genome-wide association studies data visualization

The visualization of GWAS data is critical for understanding and interpreting genetic research findings. It enables to discover patterns and connections between genetic differences and desired traits. For genomics, good visualization tools are critical for

researchers and scientists to investigate, interpret, and communicate complicated genetic relationships. One of the primary features that make GWAS data visualization valuable is its capacity to visually display large-scale genetic data. Manhattan plots and linkage disequilibrium plots provide a thorough picture of genetic variations and their relationships with phenotypes. These visualizations give researchers a bird's-eye view of the genome, enabling them to quickly discover major mutations or regions of interest. Furthermore, GWAS data visualizations allow for the discovery of hidden patterns, trends, and linkages in the data (Uffelmann et al., 2021). Researchers can use graphical representations to discover clusters of related variations, find gene-gene interactions, and investigate population-specific effects. However, there are certain difficulties in visualizing GWAS data. The sheer volume of data, including millions of genetic variants, presents scalability and interactive exploration issues (Reynolds et al., 2021). Furthermore, the intricacies of genetic relationships as well as the requirement for specific visualization approaches complicate the visualization process. Despite these difficulties, researchers continue to create novel ways and tools for successfully visualizing GWAS data and gaining significant insights from it.

With the fast progress of high-throughput genotyping technologies, the amount and complexity of GWAS datasets have expanded rapidly. Effectively visualizing these data has become critical for academics to generate valuable insights and appropriately interpret their findings. The Manhattan plot is one of the most extensively used visualization approaches in GWAS. This graph depicts the relationships between genomic locations and genetic variant p-values across the whole genome. The Manhattan plot gives a thorough overview of important genetic loci and assists in the identification of potential candidate genes responsible for phenotypic differences. For example, the Manhattan plot shows important correlations that may be missed in other representations by presenting p-values on a logarithmic scale (McCarthy et al., 2008). This enables to prioritize additional study into specific areas of interest, perhaps revealing unexpected insights into complicated traits. Moreover, heat maps are also extremely useful in GWAS visualization. Heat maps easily display complicated patterns within GWAS data by using color gradients to represent the amount of linkage or correlation. This enables researchers to swiftly discover genetic

variations linked to a certain characteristic or disease. Furthermore, heat maps may be used to compare several GWAS datasets, allowing researchers to uncover shared genetic features across populations or studies. In addition, they aid in the identification of clusters of genetic variations with comparable correlations or genes that interact in common biological pathways (Li and Dewey, 2001).

In addition, interactive visualization technologies have developed as useful GWAS analysis aids in recent years. Platforms like LocusZoom (Pruim et al., 2010) incorporate dynamic visualizations, allowing researchers to zoom in on specific genomic regions, investigate connections with various phenotypes, and insert extra information like gene annotations or functional annotations. These novel tools enable researchers to interactively analyze and refine their GWAS data. Furthermore, network visualization tools shed light on the genetic relationships and biological mechanisms at work. Network visualizations enable the discovery of critical hub genes or modules linked with specific qualities by depicting genetic variations, genes, and their interactions as nodes and edges (Shannon et al., 2003). Overall, excellent data visualization tools improve understanding and interpretation of GWAS results significantly. The mix of classic methodologies such as Manhattan plots and heat maps, as well as more dynamic and interactive tools, leads to a thorough study of GWAS data and develops a better knowledge of the genetic architecture of complex traits.

2.10.8.1 Quantile-Quantile plot

The quantile-quantile (QQ) plot is an important graphical tool used in genome-wide association studies (GWAS) to examine deviation from the expected null distribution and find probable genetic variations related with complex variables. QQ plot enables researchers to find possible outliers or genetic variations linked to the trait of interest. Furthermore, QQ plots can aid in determining the overall quality and reliability of GWAS data. GWAS investigations entail genotyping a large number of varieties and statistically assessing the relationship between millions of genetic markers and the desired phenotypic attribute. However, a variety of factors, including population structure, residual correlations, and confounding variables, might result in false-positive results. The QQ plot solves this issue successfully by comparing the observed distribution of p-values from association tests to the predicted distribution of no genuine relationships (Weine et al.,

2023). The QQ plot compares the ordered p-values on the y-axis to their predicted values on the x-axis, assuming no real correlations. Moreover Q-Q plot compares the observed quantiles of a variable to the expected quantiles from a theoretical distribution. If the points on the plot closely follow a straight line, it suggests that the model is a good fit for the data. However, if there are significant deviations or patterns in the plot, it indicates that there may be unaccounted confounding factors affecting the model's performance (Figure 7). It is produced by plotting the observed p-values ($-\log_{10}$ p-values) on the y-axis versus the projected uniform distribution of p-values on the x-axis of no connection (WTCCC, 2007; Mekonnen et al., 2021). In the absence of confounding variables, the Q-Q plot shows a solid line matching $x = y$ until it abruptly bends at the end (Zeng et al., 2015). This suggests that most of the SNPs identified in GWAS do not have a significant association with the characteristic being studied. However, it is important to consider potential confounding variables that may affect the results and interpretation of the Q-Q plot. The presence of confounding factors is suggested by the early divergence of observed p-values from null expectations; thus, including covariates in the model to compensate for the confounding factors may enhance the observed vs. expected distributions (Burghardt et al., 2017). Including covariates in the model allows for a more accurate assessment of the relationship between the independent and dependent variables by accounting for potential confounding variables. This can help to reduce bias and improve the validity of the statistical analysis (Burghardt et al., 2017). The first likely cause for the observed distribution's significant departures from predictions is a problem with phenotypic data may not fully meet the used model assumptions (Goh and Yap, 2009). Another possible cause for the discrepancies could be errors in the genotyped locus in which it could lead to an overestimation of the association between the locus and the trait being studied. By removing specific SNPs from such a region, a few marker-trait links can be enabled (Hafler et al., 2007). The existence of population structure (Q) and relatedness (K) as covariates in the model can correct the Q-Q relationship (Wen et al., 2014).

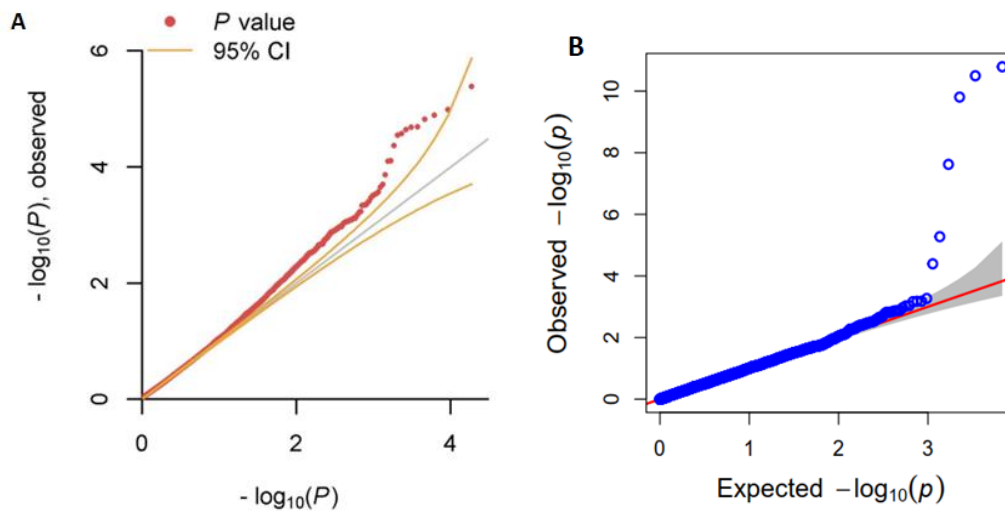


Figure 7. Q-Q plot of GWAS using, A) deviation in the observed p-value at the top end consistent with genetic influence (Source, Koshimizu et al., 2019), B) The observed $-\log(P \text{ values})$ from the fitted GWAS models (y-axis) are compared with their expected value (x-axis) under the null hypothesis of no association with the trait. Each blue dot represents a single nucleotide polymorphism; the red line is the model for no association.

2.10.8.2 The manhattan plots

Manhattan plot is named after the borough of Manhattan due to its resemblance to the skyline of tall buildings. Manhattan plot is a form of scatter plot that shows where the signal SNP is coming from and how strong it is on a whole-genome scale (McCarthy et al., 2008). It is commonly used in genome-wide association studies to identify genetic variants associated with a particular trait. Manhattan plots are an essential visual representation in genome-wide association studies (GWAS), which show the significance of genetic differences throughout the whole genome to identify genetic loci associated with a certain trait. Typically, these plots are created by graphing the p-values of genetic markers against their chromosomal locations (Figure 8). Breeders can find sections of the genome that are highly related with the trait or condition being examined by studying these maps. This data may then be utilized to delve further into the underlying biological pathways and perhaps design targeted interventions or therapies (Grace et al., 2019). The capacity of Manhattan plots to highlight sections of the genome that show strong connections with the trait under inquiry are what makes them helpful. These plot present results in a simple manner, allowing researchers to easily identify key discoveries from noise. Furthermore,

Manhattan plots aid in the identification of potential candidate regions for additional examination or replication in following studies (Uffelmann et al., 2021).

Manhattan plots have become a must-have visualization tool in genome-wide association studies (GWAS). These plots provide a detailed picture of the genome-wide relationships between genetic variations and complex traits such as disease resistance. In a standard Manhattan plot, the y-axis depicts the degree of association or statistical significance on a logarithmic scale, and the x-axis denotes genomic location, which is often represented by chromosomes. On the x-axis, genomic location is grouped based on the physical placement of genes or genetic markers along the chromosomes. This enables researchers to pinpoint specific areas or loci that may be linked to a certain characteristic or illness. The y-axis logarithmic scale aids in visualizing and comparing the strength of links across various genomic areas, with higher values suggesting more statistical significance (Delfan et al., 2023). Further, a Manhattan plot is created by graphing the negative log of each SNP's p-value on the y-axis against its corresponding genomic position on chromosomes colored in alternating types on the x-axis (Greg, 2010). By analyzing the patterns and peaks in the plot, one can gain insights into the genetic basis of complex traits and potentially identify candidate genes involved in the condition of interest. Each dot on the plot represents an SNP, with strong associations having the smallest p-values and weak associations having the largest negative logarithms. The plot provides a visual representation of the strength of association between SNPs and the variable of interest. The smaller the p-value or the larger the negative logarithm, the more significant the association is considered to be. Highly linked SNPs appear as "skyscrapers," in which these highly linked SNPs, or "skyscrapers," represent genetic variants that have a strong association with the trait or condition being studied. The horizontal line serves as a visual representation of the cutoff point for statistical significance, helping researchers identify which SNPs are most likely to be biologically relevant.

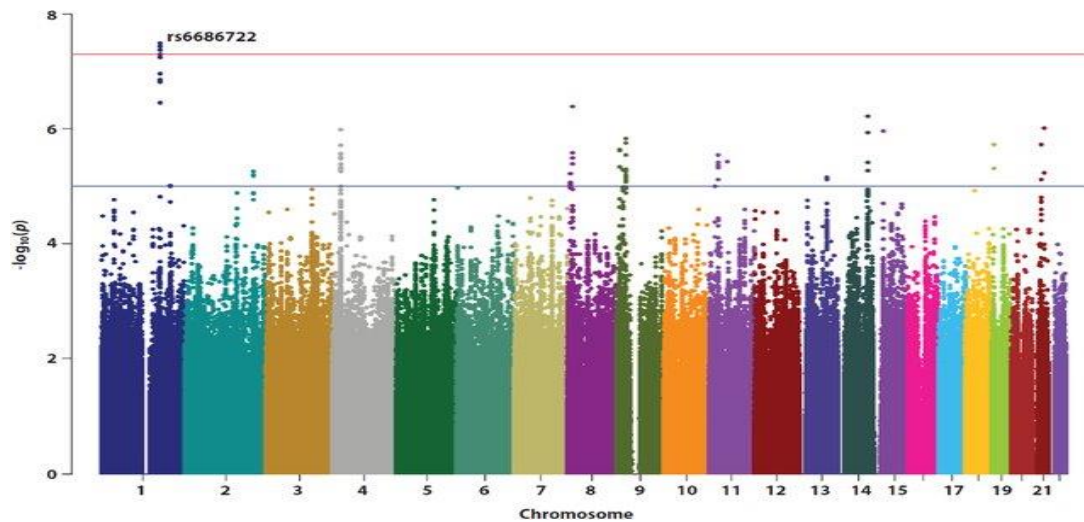


Figure 8. Manhattan plot of GWAS, Showing $-\log_{10}(p)$ value versus genomic location for autosomal chromosomes (1–21). Results show a significant association of rs6686722 genes on chromosome 1. The horizontal blue and orange lines represent p values at 1.0×10^{-5} and 5.0×10^{-8} , respectively in clinical childhood attention deficit hyperactivity disorder (Source, Koshimizu et al., 2019)

2.11 Genome wide association studies in wheat

GWAS has emerged as an effective technique for examining wheat's genomic architecture. Numerous studies have used this strategy to successfully discover critical genetic areas related to vital agronomic parameters. Cavanagh et al., (2013), for example, performed a landmark GWAS on 299 elite wheat lines, successfully finding nucleotide polymorphisms related to grain production, height, and spike length. Their findings provided credible indicators for breeding strategies aimed at increasing production. Furthermore, GWAS has improved our understanding of how wheat responds to biotic and abiotic stressors. Bajgain et al., (2016) used GWAS to find SNPs associated with resistance to fusarium head blight in a variety of wheat populations. As a result of this research, the development of resistant types is accelerated, reducing yield losses caused by this disease. Furthermore, GWAS has provided insight on drought tolerance mechanisms in wheat, with studies such as Chapman et al., (2015) identifying genetic variants related to improved water use efficiency and responsiveness to water stress. Notably, recent advances in genotyping tools and sequencing technology have hastened the speed of wheat GWAS investigations (Cavanagh et al., 2013). Furthermore, the lower cost of whole-genome sequencing has opened up new

paths for GWAS by allowing for a thorough investigation of the wheat genome and the discovery of uncommon genetic variations (Pont et al., 2019).

2.11.1 Diversity array technology for genome-wide association study

Marker technologies are well recognized to be transitioning from mostly serial tests that quantify the size of DNA fragments to hybridization-based assays with high multiplexing levels (Gupta et al., 2008). Microarray technology is often used to produce genotyping data for GWAS, allowing polymorphisms in populations to be discovered. Furthermore, microarrays require three fundamental aspects, according to Andreas and Bryce (2016): hybridization, detection, and data processing. The process of connecting complementary DNA or RNA molecules to a microarray chip, where each location on the chip carries a distinct DNA sequence, is referred to as hybridization. Detection entails identifying and quantifying the attached molecules using fluorescent labels or other techniques. Finally, data analysis is used to analyze the findings and uncover genetic changes linked to certain traits. As a result, microarrays are extensively used in genomics research to assess the expression levels of thousands of genes at the same time. They enable scientists to investigate gene expression patterns and discover genes that are upregulated or downregulated in certain traits. Hybridization signals between immobilized probes and labeled target sequences can be used to determine the relative abundance of specific genes in a sample.

DArT is a stable genotyping platform that allows for high-throughput, low-cost genotyping of a wide range of species. This method has been used successfully to explore genetic diversity, population structure, and trait connections in numerous crops. Several studies on the use of Diversity array technology (DArT) in GWAS for stripe rust resistance in wheat have been undertaken. Kumar et al., (2020) revealed significant marker-trait associations for stripe rust resistance using DArT markers in a GWAS on a diverse panel of wheat accessions. Their findings shed light on the genetic architecture of this trait by revealing multiple genomic regions connected to disease resistance. Alves-Freitas et al., (2017) investigated the genetic regulation of stripe rust resistance using a mix of DArT and functional markers. Using DArT markers in GWAS for stripe rust resistance has been used for understanding the genetic basis of this complex trait. Large populations can be tested

using DArT's high-throughput genotyping capacity, providing a rich source of genetic markers for association studies. For the GWAS, DArT markers are a prominent instrument in this process (Sánchez-Sevilla et al., 2015; Hashem et al., 2023). DArT markers are highly informative and cost-effective molecular markers that have been widely employed in genome-wide association studies (GWAS) in a variety of plants (Gawroński et al., 2016; Emrey, 2018). DArT markers, which are based on the microarray technology principle, may interrogate thousands of genomic loci at the same time. These markers cover the entire genome, allowing for the efficient discovery of genetic variants underlying phenotypes of interest. The method combines high-throughput genotyping platforms with techniques that simplify the process, such as restriction digestion and PCR amplification (Nadeem et al., 2018; Ketema et al., 2020).

The benefits of DArT markers in GWAS are: first, they provide extensive genome coverage, encompassing both coding and non-coding areas, allowing for the detection of not only gene-based variants but also regulatory elements that drive trait variation. Second, because of their robust and standardized assay design, DArT markers are highly reproducible and deliver consistent results. This makes them particularly useful for large-scale genotyping projects and population studies (Alam et al., 2018). Lastly, the low cost of DArT markers makes them accessible to researchers with limited resources, allowing for greater applicability across other species. The study by Hashem et al., (2023) is a remarkable example of the successful use of DArT markers in GWAS. DArT markers were used to identify genomic areas linked with yield-related variables. Their findings not only revealed new yield loci but also demonstrated the use and accuracy of DArT markers in large-scale association studies.

Moreover, DArT markers are the most likely molecular markers because they have two major advantages over other molecular markers: they are the most abundant form of genetic variation within genomes (Nadeem et al., 2018), and a wide range of technologies for high-throughput genotyping have now been developed. Furthermore, when compared to other molecular markers, DArT markers have been proven to be highly reproducible. As a result, they are a popular choice among researchers doing large-scale genetic investigations and breeding projects.

2.11.2 Genome-wide association studies in stripe rust

GWAS have emerged as a powerful tool for discovering genetic variations associated with complex features like stripe rust resistance. Li et al., (2019) carried out a large-scale study in which they employed GWAS to investigate the genetic architecture of stripe rust resistance in a diverse panel of wheat accessions. In the study, high-density single nucleotide polymorphism (SNP) arrays were used. This allowed the identification of a spate of significant SNP-trait associations, shedding light on the genetic basis of stripe rust resistance. The GWAS, conducted by Li et al., (2019), discovered a number of key genomic regions connected to stripe rust resistance. These regions with genes associated with defense responses, including disease resistance proteins and pathogenesis-related genes. Furthermore, novel candidate genes with potential involvement in stripe rust resistance were uncovered; furthering grasp of the underlying mechanisms in many studies (Long et al., 2019; Odilbekov et al., 2019; Cheng et al., 2020). Findings from GWAS can also help with gene discovery (Tene et al., 2022) and functional characterization (Ledesma-Ramírez et al., 2019), opening the door for the development of novel anti-stripe rust techniques.

By analyzing thousands of SNPs dispersed throughout the genome, GWAS can reveal significant relationships between SNP markers and resistance phenotypes (Wenne, 2018; Alqudah et al., 2019). This enables the identification of possible genes or genomic areas that give resistance to stripe rust. Many researchers conducted an important study in the field of stripe rust resistance (GWAS), used a panel of heterogeneous germplasm containing wheat accessions, and performed extensive genetic analysis to identify genetic components that contribute to resistance to stripe rust. They effectively discovered numerous important loci linked with stripe rust resistance by merging phenotypic data for this trait with high-density SNP marker data, giving light on the complex genetic basis of resistance to *Puccinia striiformis* f. sp. *tritici* (Maccaferri et al., 2015; Naruoka et al., 2015; Mahmood et al., 2022).

GWAS has also increased understanding of molecular pathways behind stripe rust resistance. It has enabled the identification of candidate genes implicated in diverse defensive pathways, including those involved in pathogen recognition, signal transduction,

and effector-triggered immunity (Habib et al., 2020). These findings have not only increased our understanding of host-pathogen interactions, but they have also supplied vital resources for breeders to use in developing resistant wheat varieties via marker-assisted selection (Hasan et al., 2021). Further, future research can concentrate on merging GWAS findings with functional genomics approaches to explain the precise functions of the candidate genes and their interactions in conferring substantial resistance to stripe rust (Maccaferri et al., 2015).

CHAPTER THREE

MATERIALS AND METHODS

3.1 Genetic diversity and population structure analysis of bread wheat genotypes as revealed by ISSR markers

3.1.1 Plant material

In this study, a total of 180 bread wheat genotypes, 13 commercial varieties (COV), and 167 recombinant inbred lines obtained from CIMMYT were used (Table 3). Among the 167 CIMMYT genotypes, 49 were from the International Bread Wheat Screening Nursery (IBWSN), 56 from the International Septoria Observation Nursery (ISEPON), 14 from the High Rain Wheat Yield Trial (HRWYT), 34 from the High-Rain Wheat Screening Nursery (HRWSN), five from an adaptation trial (ADT), six from the national variety trial (NVT), and the remaining three genotypes were from a preliminary variety trial (PVT). Accordingly, the research materials were grouped into eight populations (ADT, COV, HRWSN, HRWYT, IBWSN, ISEPTON, NVT, and PVT) based on their origin.

Table 3. List of bread wheat association panel used in this study

S.N	Selection History	Origin	Genotype	
			Name	Code
1	CMSS08Y00491S-099Y-099M-099NJ-37WGY-0B	MXI12-13\M47IBWSN\194	EBW001	G1
2	CMSA07Y00597S-040ZTY-040ZTM-040Y-46ZTM-010Y-0B	MXI12-13\M24ISEPTON\56	EBW002	G2
3	CMSA07M00022T-032(B=WMC221SR25HET)Y-040ZTM-074(WMC0221SR25HOM+HET)Y-55ZTM-010Y-01B-0Y	MXI12-13\M24ISEPTON\25	EBW003	G3
4	CMSS07Y01253T-099TOPM-099Y-099M-099Y-16M-0RGY	MXI11-12\M21HRWYT\24	EBW004	G4
5	CMSS08Y00924T-099TOPM-099Y-099M-099NJ-099NJ-10RGY-0B	MXI12-13\M25HRWSN\1053	EBW005	G5
6	CMSS08Y00224S-099Y-099M-099NJ-099NJ-1WGY-0B	MXI12-13\M47IBWSN\81	EBW006	G6
7	CMSS08Y00704T-099TOPM-099Y-099Y-11M-0WGY	MXI12-13\M47IBWSN\247	EBW007	G7

8	CMSS08B00861T-099TOPY-099M-099Y-13M-0WGY	MXI12-13\M47IBWSN\722	EBW008	G8
10	Commercial Cultivar	Bika	Bika	G10
11	CMSA08M00458S-040ZTM-050Y-50ZTM-010Y-0B	MXI12-13\M25HRWSN\1174	EBW011	G11
12	CMSS93B00686S-12Y-010M-010Y-010M-7Y-1M-0Y-3SJ-0Y-2PZ-0Y	MXI12-13\M24ISEPTON\102	EBW012	G12
13	Addaptation rial	Adap	EBW013	G13
14	Commercial Cultivar	Meraro	Meraro	G14
15	CMSA08M00432S-040M-0NJ-10Y-0B	MXI12-13\M25HRWSN\1166	EBW015	G15
16	CMSA08M00466S-040ZTM-050Y-47ZTM-010Y-0B	MXI12-13\M25HRWSN\1175	EBW016	G16
17	LOCAL CHECK	\0	EBW017	G17
18	CMSS08B00911T-099TOPY-099M-099NJ-12WGY-0B	MXI12-13\M47IBWSN\779	EBW018	G18
19	CMSS08B00422S-099M-099NJ-5RGY-0B	MXI12-13\M25HRWSN\1100	EBW019	G19
20	CMSS08Y00611T-099TOPM-099Y-099M-099Y-2M-0WGY	MXI12-13\M47IBWSN\208	EBW020	G20
21	Commercial Cultivar	Alidoro	Alidoro	G21
22	Commercial Cultivar	Medawolabu	Medawolabu	G22
23	CMSS06Y00586T-099TOPM-099Y-099ZTM-099Y-099M-5WGY-0B	MXI11-12\SELC23ISEPTO\22	EBW023	G23
24	CMSS08B00772T-099TOPY-099M-099Y-21M-0WGY	MXI12-13\M47IBWSN\655	EBW024	G24
25	CMSS08Y01110T-099M-099Y-099M-099NJ-7WGY-0B	MXI12-13\M47IBWSN\415	EBW025	G25
26	Addaptation rial	Adap	EBW026	G26
27	CMSS08Y00869T-099TOPM-099Y-099M-099Y-22M-0WGY	MXI12-13\M47IBWSN\335	EBW027	G27
28	CMSS07Y00299S-0B-099Y-099M-099Y-2M-0WGY	MXI12-13\M24ISEPTON\69	EBW028	G28
29	CMSS08Y00477S-099Y-099M-099NJ-7WGY-0B	MXI12-13\M47IBWSN\18	EBW029	G29

		5		
30	CMSS08Y00483S-099Y-099M-099Y-11M-0WGY	MXI12-13\M47IBWSN\188	EBW030	G30
31	CMSS08B00777T-099TOPY-099M-099NJ-099NJ-5RGY-0B	MXI12-13\M25HRWSN\1127	EBW031	G31
32	CMSA07M00376S-040ZTM-040ZTY-63ZTM-010Y-02B-0Y	MXI11-12\M31SAWSN\266	EBW032	G32
33	Commercial Cultivar	Huluka	Huluka	G33
34	CMSS07B00311S-099M-099Y-099M-4WGY-0B	MXI12-13\M24ISEPTON\89	EBW034	G34
35	CMSS07Y00774T-099TOPM-099Y-099M-099NJ-099NJ-6WGY-0B	MXI12-13\M24ISEPTON\74	EBW035	G35
36	CMSS08B00966T-099TOPY-099M-099Y-099B-17RGY-0B	MXI12-13\M25HRWSN\1138	EBW036	G36
37	CMSA08Y00045T-024(CRE1)B-050ZTY-067(CRE1)ZTM-03Y-01B-0Y	MXI12-13\M24ISEPTON\32	EBW037	G37
38	National Variety Trial 3	NVT3	EBW038	G38
39	CMSS08B00337S-099M-099NJ-099NJ-29WGY-0B	MXI12-13\M47IBWSN\492	EBW039	G39
40	Commercial Cultivar	Kingbird	Kingbird	G40
41	CMSS08B00381S-099M-099Y-1M-0RGY	MXI12-13\M25HRWSN\1099	EBW041	G41
42	CMSS07B00191S-099M-099Y-099M-22WGY-0B	MXI12-13\M24ISEPTON\85	EBW042	G42
43	CMSS08Y00872T-099TOPM-099Y-099M-099NJ-099NJ-9RGY-0B	MXI12-13\M25HRWSN\1041	EBW043	G43
44	CMSS07Y00815T-099TOPM-099Y-099M-099Y-7M-0RGY	MXI11-12\M21HRWYT\16	EBW044	G44
45	CMSA07M00634S-040ZTM-040ZTY-54ZTM-010Y-01B-0Y	MXI12-13\M24ISEPTON\12	EBW045	G45
46	CMSS08B00974T-099TOPY-099M-099Y-099B-38WGY-0B	MXI12-13\M47IBWSN\811	EBW046	G46
47	CMSA08Y00065T-099B-050Y-050ZTM-050Y-14BMX-010Y-0B	MXI12-13\M25HRWSN\1141	EBW047	G47

48	Addaptation rial	Adap	EBW048	G48
49	CMSS08Y00127S-099Y-099M-099NJ-30WGY-0B	MXI12-13\M47IBWSN\25	EBW049	G49
50	CMSS08B00475S-099M-099Y-17M-0WGY	MXI12-13\M47IBWSN\517	EBW050	G50
51	National Variety Trial 4	NVT4	EBW051	G51
52	CMSS08B00283S-099M-099NJ-099NJ-8WGY-0B	MXI12-13\M47IBWSN\470	EBW052	G52
53	CMSA07M00371S-040ZTM-040ZTY-19ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\2	EBW053	G53
54	CMSA08Y00469S-050Y-040M-0NJ-20Y-0B	MXI12-13\M25HRWSN\147	EBW054	G54
55	CMSS08Y00627T-099TOPM-099Y-099M-099NJ-5WGY-0B	MXI12-13\M47IBWSN\220	EBW055	G55
56	Plimenary Variety Trial	PVT	EBW056	G56
57	CMSA07M00441S-040ZTM-040ZTY-20ZTM-010Y-01B-0Y	MXI12-13\M24ISEPTON\4	EBW057	G57
58	CMSS07B00236S-099M-099Y-099M-13WGY-0B	MXI11-12\M46IBWSN\202	EBW058	G58
59	CMSS06Y01171T-099TOPM-099Y-099ZTM-099Y-099M-8WGY-0B	MXI11-12\M34ESWYT\218	EBW059	G59
60	CMSS07Y00346S-0B-099Y-099M-099NJ-099NJ-3WGY-0B	MXI12-13\M24ISEPTON\70	EBW060	G60
61	Plimenary Variety Trial	PVT	EBW061	G61
62	National Variety Trial 2	NVT2	EBW062	G62
63	Addaptation rial	Adap	EBW063	G63
64	CMSS06Y00631T-099TOPM-099Y-099ZTM-099Y-099M-2WGY-0B	MXI11-12\SELC23ISEPTO\31	EBW064	G64
65	CMSS08Y00871T-099TOPM-099Y-099M-099NJ-099NJ-2WGY-0B	MXI12-13\M47IBWSN\345	EBW065	G65
66	CMSS08Y00182S-099Y-099M-099NJ-099NJ-2WGY-0B	MXI12-13\M47IBWSN\69	EBW066	G66
67	CMSS93B00686S-12Y-010M-010Y-010M-7Y-1M-0Y-3SJ-0Y-2PZ-0Y	MXI10-11\C22ISEPTON\102	EBW067	G67
68	CMSA07M00443S-040ZTM-040ZTY-47ZTM-010Y-02B-0Y	MXI11-12\M21HRWYT-	EBW068	G68

		RF\2		
69	CMSA07Y01090T-045B-040Y-040ZTM-040Y-20ZTM-010Y-0B	MXI12-13\M24ISEPTON\34	EBW069	G69
70	CMSS07B00264S-099M-099NJ-099NJ-8WGY-0B	MXI12-13\M24ISEPTON\88	EBW070	G70
71	Commercial Cultivar	Danda'a	Danda'a	G71
72	CMSS08Y00491S-099Y-099M-099NJ-099NJ-11WGY-0B	MXI12-13\M47IBWSN\196	EBW072	G72
73	CMSS08Y00627T-099TOPM-099Y-099M-099NJ-6WGY-0B	MXI12-13\M47IBWSN\221	EBW073	G73
74	CMSA08Y00109T-099B-050Y-050ZTM-050Y-42BMX-010Y-0B	MXI12-13\M47IBWSN\823	EBW074	G74
75	CMSS08B00777T-099TOPY-099M-099NJ-099NJ-12RGY-0B	MXI12-13\M25HRWSN\1128	EBW075	G75
76	CMSS07Y00213S-0B-099Y-099M-099Y-20M-0WGY	MXI12-13\M24ISEPTON\65	EBW076	G76
77	CMSA07M00022T-032(B=WMC221SR25HET)Y-040ZTM-074(WMC0221SR25HOM+HET)Y-9ZTM-010Y-01B-0Y	MXI11-12\M31SAWSN\93	EBW077	G77
78	CMSS07Y00672T-099TOPM-099Y-099M-099Y-36M-0WGY	MXI12-13\M24ISEPTON\71	EBW078	G78
79	CMSS07B00614T-099TOPY-099M-099Y-099M-7WGY-0B	MXI12-13\M24ISEPTON\92	EBW079	G79
80	Commercial Cultivar	Et-13A2	Et-13A2	G80
81	CMSS08Y01116T-099M-099Y-099M-099NJ-099NJ-14WGY-0B	MXI12-13\M47IBWSN\418	EBW081	G81
82	CMSA07Y00273S-040ZTY-040ZTM-040Y-30ZTM-010Y-0B	MXI12-13\M24ISEPTON\55	EBW082	G82
83	CMSA07M00455S-040M-0NJ-0NJ-2Y-0B	MXI12-13\M24ISEPTON\42	EBW083	G83
84	CMSS06B00001S-0Y-099ZTM-099Y-099M-8WGY-0B	MXI12-13\M24ISEPTON\99	EBW084	G84
85	CMSS07Y00174S-0B-099Y-099M-099Y-22M-0WGY	MXI11-12\M34ESWYT\18	EBW085	G85

86	CMSA08M00446S-040ZTM-050Y-5ZTM-010Y-0B	MXI12-13\M25HRWSN\170	EBW086	G86
87	CMSS07B00151S-099M-099Y-099M-7WGY-0B	MXI12-13\M24ISEPTON\83	EBW087	G87
88	CMSS08Y00224S-099Y-099M-099NJ-099NJ-16RGY-0B	MXI12-13\M25HRWSN\1011	EBW088	G88
89	CMSS07B00231S-099M-099Y-099M-47WGY-0B	MXI12-13\M24ISEPTON\86	EBW089	G89
90	CMSS07Y01307T-099Y-7M-0Y-3B-0Y	MXI11-12\M46IBWSN\320	EBW090	G90
91	CMSS97M03642T-040Y-020Y-030M-020Y-040M-7Y-3M-0Y	MXI12-13\M24ISEPTON\101	EBW091	G91
92	CMSA07WM00080S-050Y-040ZTM-040ZTY-78ZTM-010Y-02B-0Y	MXI11-12\M1STSWYPT\22	EBW092	G92
93	CMSA07M00065T-029(AWW5L7BO1HET&CRE1M19NEG)Y-040ZTM-040Y-36ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\23	EBW093	G93
94	CMSS06Y00920T-099TOPM-099Y-099ZTM-099Y-099M-16WGY-0B	MXI11-12\SELC23ISEPTO\36	EBW094	G94
95	CMSS06Y00706T-099TOPM-099Y-099ZTM-099NJ-099NJ-7WGY-0B	MXI12-13\M24ISEPTON\96	EBW095	G95
97	CMSS08Y00224S-099Y-099M-099NJ-099NJ-8RGY-0B	MXI12-13\M25HRWSN\1009	EBW097	G97
98	CMSA07Y00598S-040ZTY-040ZTM-040Y-5ZTM-010Y-0B	MXI12-13\M24ISEPTON\36	EBW098	G98
99	CMSS08Y00224S-099Y-099M-099NJ-099NJ-19RGY-0B	MXI12-13\M25HRWSN\1012	EBW099	G99
100	CMSS08Y00174S-099Y-099M-099NJ-099NJ-17WGY-0B	MXI12-13\M47IBWSN\64	EBW100	G100
101	CMSA08Y00530S-050Y-040M-0NJ-7Y-0B	MXI12-13\M47IBWSN\847	EBW101	G101
102	CMSS08B00771T-099TOPY-099M-099NJ-099NJ-21WGY-0B	MXI12-13\M47IBWSN\653	EBW102	G102
103	CMSA07M00043T-050Y-040ZTM-040ZTY-92ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\	EBW103	G103

		13		
104	CMSS07Y00032S-0B-099Y-099M-099Y-2M-0WGY	MXI12-13\M24ISEPTON\63	EBW104	G104
105	CMSS07Y00963T-099TOPM-099Y-099M-099Y-32M-0WGY	MXI11-12\M34ESWYT\72	EBW105	G105
106	CMSS07Y00255S-0B-099Y-099M-099NJ-099NJ-14WGY-0B	MXI12-13\M24ISEPTON\66	EBW106	G106
107	CMSS06Y00117S-0B-099Y-099ZTM-099Y-099M-12WGY-0B	MXI11-12\SELC23ISEPTO\12	EBW107	G107
108	CMSS08B00391S-099M-099Y-10M-0WGY	MXI12-13\M47IBWSN\496	EBW108	G108
109	Plimentary Variety Trial	PVT	EBW109	G109
110	CMSS06Y00946T-099TOPM-099Y-099ZTM-099Y-099M-13WGY-0B	MXI12-13\M24ISEPTON\97	EBW110	G110
111	CMSS08Y00220S-099Y-099M-099NJ-6RGY-0B	MXI12-13\M25HRWSN\1007	EBW111	G111
112	CMSA07M00644S-040M-0NJ-0NJ-5Y-0B	MXI12-13\M24ISEPTON\44	EBW112	G112
113	CMSS07Y00815T-099TOPM-099Y-099M-099Y-7M-0RGY	MXI11-12\M21HRWYT\16	EBW113	G113
114	CMSA08Y00378S-050Y-050ZTM-050Y-2BMX-010Y-0B	MXI12-13\M47IBWSN\830	EBW114	G114
115	CMSS08Y00627T-099TOPM-099Y-099M-099NJ-37WGY-0B	MXI12-13\M47IBWSN\224	EBW115	G115
116	CMSS08Y00182S-099Y-099M-099NJ-099NJ-9WGY-0B	MXI12-13\M47IBWSN\74	EBW116	G116
117	CMSS08Y00623T-099TOPM-099Y-099M-099NJ-099NJ-7WGY-0B	MXI12-13\M47IBWSN\217	EBW117	G117
118	CMSA07Y00950T-8B-040Y-040ZTM-040Y-10ZTM-010Y-0B	MXI12-13\M24ISEPTON\62	EBW118	G118
119	CMSS07Y00704T-099TOPM-099Y-099M-099NJ-099NJ-9WGY-0B	MXI12-13\M24ISEPTON\73	EBW119	G119
120	CMSA07M00158T-056(CSLV34HET)Y-040ZTM-055(CSLV34HOM+HET)Y-17ZTM-010Y-01B-0Y	MXI12-13\M24ISEPTON\26	EBW120	G120

121	CMSS08B00196S-099M-099NJ-099NJ-36RGY-0B	MXI12-13\M25HRWSN\1074	EBW121	G121
122	CMSS06Y00920T-099TOPM-099Y-099ZTM-099Y-099M-36WGY-0B	MXI11-12\SELC23ISEPTO\37	EBW122	G122
123	CMSS08B00776T-099TOPY-099M-099NJ-099NJ-21RGY-0B	MXI12-13\M25HRWSN\1124	EBW123	G123
124	CMSA08M00424S-040ZTM-050Y-13ZTM-010Y-0B	MXI12-13\M25HRWSN\1162	EBW124	G124
125	CMSA07WM00080S-050Y-54ZTM-08Y-0B-03Y-(01B)-0Y	MXI11-12\M1STSWYPT\43	EBW125	G125
126	CMSS06Y00952T-099TOPM-099Y-099ZTM-099Y-099M-5WGY-0B	MXI11-12\SELC23ISEPTO\44	EBW126	G126
127	Commercial Cultivar	Paven-76	Paven-76	G127
128	CMSA07M00470S-040ZTM-040ZTY-15ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\20	EBW128	G128
129	CMSS08B00776T-099TOPY-099M-099NJ-099NJ-14RGY-0B	MXI12-13\M25HRWSN\1123	EBW129	G129
130	CMSA07M00443S-040ZTM-040ZTY-47ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\51	EBW130	G130
131	CMSS07B00248S-099M-099Y-099M-4WGY-0B	MXI11-12\M46IBWSN\215	EBW131	G131
132	CMSS08Y00351S-099Y-099M-099NJ-099NJ-4RGY-0B	MXI12-13\M25HRWSN\1023	EBW132	G132
133	CMSS08Y00872T-099TOPM-099Y-099M-099NJ-099NJ-4RGY-0B	MXI12-13\M25HRWSN\1040	EBW133	G133
134	CMSS08Y00627T-099TOPM-099Y-099M-099NJ-16WGY-0B	MXI12-13\M47IBWSN\222	EBW134	G134
135	CMSA08Y00556S-050Y-050ZTM-050Y-45BMX-010Y-0B	MXI12-13\M25HRWSN\1150	EBW135	G135
136	CMSS08B00919T-099TOPY-099M-099NJ-099NJ-7RGY-0B	MXI12-13\M25HRWSN\1137	EBW136	G136
137	CMSS08Y00182S-099Y-099M-099NJ-099NJ-8WGY-0B	MXI12-13\M47IBWSN\73	EBW137	G137
138	CMSA07WM00080S-050Y-54ZTM-	MXI11-	EBW138	G138

	08Y-0B-08Y-(03B&04B)-0Y	12\M1STSWYPT\8		
139	CMSA08M00445S-040ZTM-050Y-47ZTM-010Y-0B	MXI12-13\M25HRWSN\1169	EBW139	G139
140	CMSS07B00869T-099TOPY-099M-099Y-099M-1WGY-0B	MXI12-13\M24ISEPTON\95	EBW140	G140
141	CMSS08Y00224S-099Y-099M-099NJ-099NJ-4RGY-0B	MXI12-13\M25HRWSN\1008	EBW141	G141
142	CMSS08Y00234S-099Y-099M-099NJ-099NJ-20WGY-0B	MXI12-13\M47IBWSN\95	EBW142	G142
143	CMSA07WM00080S-050Y-040ZTM-040ZTY-8ZTM-010Y-01B-0Y	MXI11-12\M1STSWYPT\20	EBW143	G143
144	CMSS07B00024S-099M-099Y-099M-21RGY-0B	MXI11-12\M24HRWSN\32	EBW144	G144
145	CMSS08Y00220S-099Y-099M-099Y-11M-0WGY	MXI12-13\M47IBWSN\78	EBW145	G145
146	CMSS08B00763T-099TOPY-099M-099NJ-19WGY-0B	MXI12-13\M47IBWSN\644	EBW146	G146
147	CMSA07M00445S-040ZTM-040ZTY-75ZTM-010Y-01B-0Y	MXI12-13\M24ISEPTON\18	EBW147	G147
148	CMSA07M00403S-040ZTM-040ZTY-21ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\16	EBW148	G148
149	Commercial Cultivar	Sofomor	Sofomor	G149
150	CMSA08M00124T-050Y-040ZTM-050Y-8ZTM-010Y-0B	MXI12-13\M25HRWSN\1154	EBW150	G150
151	CMSA08M00052T-050Y-040M-0NJ-10Y-0B	MXI12-13\M25HRWSN\1152	EBW151	G151
152	Commercial Cultivar	KI6295-4A	KI6295-4A	G152
153	CMSA08Y00083T-099B-050Y-050ZTM-050Y-41BMX-010Y-0B	MXI12-13\M25HRWSN\1144	EBW153	G153
154	CMSS06B00201S-0Y-099ZTM-099Y-099M-15WGY-0B	MXI11-12\SELC23ISEPTO\1	EBW154	G154
155	CMSS06Y00672T-099TOPM-099Y-099ZTM-099Y-099M-10WGY-0B	MXI11-12\SELC23ISEPTO\34	EBW155	G155
156	CMSA07M00365S-040M-0NJ-0NJ-4Y-0B	MXI12-13\M24ISEPTON\58	EBW156	G156

157	CMSA07M00453S-040ZTM-040ZTY-13ZTM-010Y-01B-0Y	MXI11-12\M21HRWYT-RF\4	EBW157	G157
158	CMSA07WM00080S-050Y-23ZTM-03Y-0B-07Y-(01B&02B)-0Y	MXI11-12\M1STSWYPT\34	EBW158	G158
159	National Variety Trial 6	NVT6	EBW159	G159
160	CMSS08B00233S-099M-099NJ-099NJ-25RGY-0B	MXI12-13\M25HRWSN\1075	EBW160	G160
161	CMSS07B00326S-099M-099Y-099M-16WGY-0B	MXI11-12\M46IBWSN\229	EBW161	G161
162	CMSS07Y00066S-0B-099Y-099M-099Y-43M-0WGY	MXI11-12\M46IBWSN\13	EBW162	G162
163	CMSA08Y00025T-095(1A1R)B-050ZTY-075(1A1R)ZTM-03Y-02B-0Y	MXI12-13\M24ISEPTON\31	EBW163	G163
164	CMSS08Y00235S-099Y-099M-099NJ-1WGY-0B	MXI12-13\M47IBWSN\96	EBW164	G164
165	National Variety Trial 2	NVT2	EBW165	G165
166	National Variety Trial 5	NVT5	EBW166	G166
167	LOCAL CHECK	\\0	EBW167	G167
168	Addaptation rial	Adap	EBW168	G168
169	CMSS08Y00224S-099Y-099M-099NJ-099NJ-11WGY-0B	MXI12-13\M47IBWSN\82	EBW169	G169
170	CMSS08B00776T-099TOPY-099M-099NJ-099NJ-6RGY-0B	MXI12-13\M25HRWSN\1122	EBW170	G170
171	CMSS06Y00672T-099TOPM-099Y-099ZTM-099Y-099M-8WGY-0B	MXI11-12\SELC23ISEPTO\33	EBW171	G171
172	CMSA08Y00061T-079(1A1RSR26)B-050ZTY-026(1A1RSR26)ZTM-02Y-01B-0Y	MXI12-13\M24ISEPTON\33	EBW172	G172
173	Commercial Cultivar	K-6290-Bulk	K-6290-Bulk	G173
174	CMSA05M00149S-040ZTM-040ZTY-11ZTM-02Y-0B	MXI11-12\SELC23ISEPTO\81	EBW174	G174
175	Commercial Cultivar	Hogana	Hogana	G175
176	CMSS06B00201S-0Y-099ZTM-099Y-099M-8WGY-0B	MXI11-12\M34ESWYT\224	EBW176	G176
177	CMSS08Y00627T-099TOPM-099Y-099M-099NJ-38WGY-0B	MXI12-13\M47IBWSN\225	EBW177	G177
178	CMSA07M00376S-040ZTM-040ZTY-15ZTM-010Y-02B-0Y	MXI12-13\M24ISEPTON\	EBW178	G178

		50		
179	CMSS08Y00182S-099Y-099M-099NJ-099NJ-6WGY-0B	MXI12-13\M47IBWSN\72	EBW179	G179
180	CMSS07Y00963T-099TOPM-099Y-099M-099Y-32M-0WGY	MXI12-13\M24ISEPTON\78	EBW180	G180

3.1.2 Genomic DNA extraction

For genomic DNA extraction, the study wheat plants were grown in greenhouse conditions at Addis Ababa University. Genomic DNA (gDNA) was extracted from 50 mg 2-week-old silica gel dried leaf samples pooled from five plants per genotype using a modified cetyl trimethyl ammonium bromide (CTAB) procedure (Ogbonnaya et al., 2001; Mekonnen et al., 2017). The quantity and quality of the extracted DNA were checked using Nanodrop spectrophotometry (thermo scientific™ nanodrop™ 2000/2000c spectrophotometers) and electrophoresis on a 1% agarose gel, respectively.

3.1.3 ISSR genotyping and data scoring

Thirty ISSR primers ranging from 16 to 25 base pairs (bp) in length and representing di, tri, and tetramer repetitions were tested for polymorphism and reproducibility. Out of the 30 primers examined, 10 reproducible ones with distinct banding patterns were used. These were dissolved in 10pmol/l concentration of sterilized, double-distilled water. For optimum amplification, different concentrations of template DNA and different amount of dNTPs, primers and Taq polymerase were examined. Polymerase chain reaction (PCR) was carried out in a total volume of 20 µL containing 2.5 µL of 10 x PCR buffer, 2.5 µL MgCl₂ (25 mM), 0.5 µL dNTP mixture (10 mM), 0.5 µL primer (15 pmole/µL), 0.3 µL *Taq* DNA polymerase (1 U/µL), 2 µL of template DNA (80 ng/µL) and 11.7µL double-distilled water. Optimization of the PCR condition (annealing temperature) was performed on a Biometra 2003 T3 thermocycler (USA). The PCR amplification program involved an initial denaturation at 94 °C for 5 min, followed by 40 cycles of denaturation at 94 °C for 1 min, optimized primer annealing conditions (45-52 °C for 1 min), and primer extension at 72 °C for 2 min, followed by a final extension step of 10 min at 72 °C. Amplification products were fractionated by loading 10µl amplification product of each sample with 2µl 6X loading dye on 1.67 % agarose gel electrophoresis supplemented with ethidium bromide in 1x TBE buffer at 120 V for 2 hr. The gel was visualized under UV light and subsequently

photographed using a BIO-RAD Gel Doc TM EZ Imaging System. A 100 bp DNA ladder was used to estimate the amplification size (Wilson and Walker, 2005).

For scoring purpose, an ISSR marker was used as dominant marker, and hence, each locus was considered as a bi-allelic locus with one amplifiable and one null allele. Scoring was performed manually for each primer based on presence (1) and absence (0) or ambiguous (?), and each band was regarded as a locus. The band scoring resulted in a “0” and “1” data matrix that was used for further analysis.

3.1.4 Data analysis

Different statistical software packages were used to analyze genetic diversity and population structure of the bread wheat genotypes. Locus based diversity parameters including number of observed alleles (N_a), effective number of alleles (N_e), Shannon's information statistic (I), Nei's genetic diversity (h), total genetic diversity (H_T), genetic differentiation (H_S), genetic differentiation statistics by locus (G_{st}), estimate of the number of migrants (gene flow) (N_m) and percent polymorphic loci (PPL) were computed using POPGENE version 1.31 software (Yeh et al., 1999). Within population genetic diversity parameters such as number of observed alleles (N_a), Effective number of alleles (N_e), Shannon's Information index (I), Nei's genetic diversity (h) and Percent of polymorphic Loci (PPL) across loci were computed using GenAlEx ver. 6.501 software (Nei, et al., 1983; Peakall and Smouse, 2006). The polymorphism information content (PIC) was computed using the formula: $PIC = 1 - [2f + (1-f)^2]$, where f is the frequency of occurrence of polymorphic bands in different primers. GenAlEx ver. 6.501 software was used to compute the analysis of molecular variance (AMOVA) and the estimation of the variance components. Clustering was carried out based on the unweighted pair group method with arithmetic mean (UPGMA) using molecular evolutionary genetics analysis (MEGA) software (Sudhir et al., 2018). Bayesian model-based clustering with presumed K populations was employed for 180 wheat germplasm using STRUCTURE, version 2.3.4 (Pritchard et al., 2000; Hubisz et al., 2009). The run parameters were 80,000 iterations of burn-in with 80,000 Monte Carlo Markov Chain (MCMC) iterations. Using web-based STRUCTURE HARVESTER (Earl and VonHoldt, 2011), K values from 1 to 10 were used

with 15 independent runs for each K. A bar plot for the optimum K was determined using the Clumpak beta version (Kopelman et al., 2015).

3.2 Genetic variability, heritability and GxE interaction of bread wheat genotypes

3.2.1 Field based phenotyping

The field experiment was conducted at three selected sites in Ethiopia, namely, Kulumsa Agricultural Research Center (KARC), Meraro (substation of KARC) and Holeta Agricultural Research Center (Supplementary Table 1). All locations represent major wheat-growing areas in the central highlands of Ethiopia. In these experiments, 180 bread wheat genotypes (13 commercial varieties and 167 recombinant inbred lines) were evaluated across these locations in the 2020/21 main cropping season. These 180 bread wheat genotypes constituted eight populations: Adaptation Trial (ADT), Commercial varieties (COV), High rain weed trial screening nursery (HRWSN), High rain weed yield trial (HRWYT), International bread wheat screening nursery (IBWSN), International Septoria observation nursery (ISEPTON) National variety trial (NVT) and Primary variety trial (PVT). An alpha-lattice design was used to evaluate the germplasm in two replications with six sub-blocks (Supplementary Table 1). Each accession was sown manually in 1m length, with 20 cm spacing between rows and 40 cm between entries. Spaces between blocks and replications were maintained at 1.50 m long. A seed rate of 150 kg ha⁻¹ and fertilizer rates of 100 and 75 kg ha⁻¹ N and P₂O₅, respectively, were applied to all experiments. Weeding was done three times by hand. The origin and pedigree of these materials are presented in (Table 3). The agro-morphological traits considered for the multivariate analysis were: days to 50% heading (DH), days to 50% flowering (DF), days to maturity (DM), thousand kernel weight (TKW = weight of 1,000 kernels in grams), grain yield per plot (GYPP), plant height (PH), spike length (SL), flag leaf area (LA), number of spikelets per spike (NSsS), number of kernels per spikelet (NKSs), number of kernel per spike (NKS) and spike weight (SW). Data were measured from five individual plants in each plot on the 12 agro-morphological traits considered for the study.

3.2.2 Data analysis

3. 2.2.1 Analysis of genetic parameters

The data collected for each quantitative trait were subjected to analysis of variance (ANOVA) done by means of Genestat software 18th version (VSN International, 2015) using mixed effect model by considering germplasm as fixed effect and the environment/location random effect. The phenotypic and genotypic variances and coefficients of variation were estimated according to the method d by Mathew (2015) as follows:

$$\text{Environmental variance } (\delta^2 e) = MSe \quad (1)$$

$$\text{Genotypic variance } (\delta^2 g) = \frac{MSg - MSge}{rl} \quad (2)$$

$$\text{Phenotypic variance } (\delta^2 p) = \delta^2 g + \delta^2 gl + \delta^2 e \quad (3)$$

$$\text{Where } \delta^2 e = \frac{MSe}{rl}, GCV = \frac{\sqrt{\delta^2 g}}{\bar{X}} * 100, PCV = \frac{\sqrt{\delta^2 p}}{\bar{X}} * 100 \quad (4)$$

Legends: $\delta^2 g$ = genetic variance, MSe= mean square error variance (environmental variance or $\delta^2 e$), MSg = mean square of genotypes, MSge = mean square of germplasm by environment interaction, $\delta^2 p$ = Phenotypic variance, l= number of locations and r = number of replications.

Broad sense heritability (h^2), Genetic advance (GA) and Genetic advance as a percent of means (GAM) of genotypes across environments were calculated based on Bello et al., (2012).

$$\text{Broad sense heritability } (h^2) = \frac{\delta^2 g}{\delta^2 p} \quad (5)$$

$$\text{Genetic advance (GA)} = \sqrt{\delta^2 p} * H^2 \quad (6)$$

$$\text{Genetic advance as \% of mean (GAM)} = \frac{GA}{\bar{X}} * 100 \quad (7)$$

Legends: $\delta^2 g$ = genetic variance, $\delta^2 p$ = Phenotypic variance and $\bar{X}$ = mean of the character being evaluated.

To estimate the optimal number of clusters and carry out the grouping (Maechler et al., 2019) cluster analysis was conducted in R programming software using ggplot2 (Wickham, 2016) and factoextra (Alboukadel and Fabian, 2020) packages. Similarly, principal component analysis was computed using ggplot2 (Wickham, 2016), factoextra (Alboukadel

and Fabian, 2020) and agricolae (Felipe de, 2020) packages. Correlation analysis: both phenotypic and genotypic correlations among the different parameters were analyzed using META-R (Multi Environment Trial Analysis with R for Windows) Version 6.04 software (Alvarado et al., 2015). Moreover, path analysis was performed using in R software the virility package (Raj et al., 2020).

3.2.2.2 Genotype by environment interaction analysis

Genotype by environment interaction analysis was carried out based on AMMI and GGE analysis with GEA-R (R 4.0 version for Windows) (GEA-R, 2016). GYPP data of 180 genotypes from three locations was evaluated using AMMI analysis (Pacheco et al., 2015). For GGE biplot analysis, the top 33 genotypes were used according to the mean grain yield results of the three environments. The biplot type was chosen using criteria set by Yan and Kang (2003). Furthermore, GGE biplots were performed to identify mega - environments and superior genotypes using GEA-R (2016). Metan (Olivoto et al., 2020) and ggplot2 (Wickham, 2016) packages and the GenStat version18 software (VSN International, 2015) were also used to generate the GGE biplot.

3.3 Virulence variability of Ethiopian *P. striiformis* isolates and seedling resistance in bread wheat genotypes

3.3.1 Plant materials

A set of 178 genotypes, including 156 bread wheat genotypes and 12 selected commercial bread wheat cultivars of Ethiopia (Table 3) and 10 differential lines (Table 4) were used in this study to determine the infection behavior of *P. striiformis* isolates obtained from the main wheat growing regions of Ethiopia at seedling stage. Wheat commercial cultivars were obtained from the wheat breeding program of Ethiopia's Kulumsa Agricultural Research Centre (KARC). The 156 bread wheat genotypes were received from Mexico's International Maize and Wheat Improvement Centre (CMMYT) (Supplemental Table 3). Ten differential lines with known Yr gene(s) from KARC, which were obtained from Ethiopian wheat breeders, were used to analyze resistance genes (Table 4). Pathotyping fungus isolates was accomplished by monitoring how different lines reacted to the isolates.

Table 4. List of Ethiopian released bread wheat cultivars tested for *P. striiformis* resistance

Wheat Genotype	Origin	Selection center	Pedigree	Year of Release
Et-13 A2	Ethiopia	Holeta	UQ 105SEL. X ENKOY	1981
Meraro	Ethiopia	Kulumsa	M/4/HAR 1709/ 3/M//24/E	2005
Alidoro	USA	Holeta	HK-14-R251	2007
Huluka	ICARDA	Kulumsa	UTQUE96/3/PYN/BAU//MILAN	2012
Kingbird	NA	Kulumsa	TAM-200/TUI/6/PABON-F 76//CARIANC	2015
Hoggena	ICARDA	Kulumsa	PYN/BAU//MILAN	2011
Bika	CIMMYT	EIAR	PASTOR//HXL7573/2*BAU/3WBLL1	2014
Medawolabu	Ethiopia	EIAR	TECOLOTE/3/FRONTANA(FN)/(TH)T HATCHER/2*NARINO- 59/4/(SIB)BOLAN	2000
Paven-76	CIMMYT	EIAR	VICAM-71//CIANO-67/SIETE- CERROS- 66/3/KALYANSONA/BLUEBIRD	1982
Sofomor	CIMMYT	EIAR	LIRA/TANAGER	2000
K-6290-Bulk	CIMMYT	EIAR	AFRICA/MAYO-48//2*ROMANY	1977
KI6295-4A	CIMMYT	EIAR	ROMANY//GABO/GAMENYA	1980

Table 5. List of 10 bread wheat cultivars possessing known Yr gene(s) (differential lines)

Differential lines	Yr Gene	Origin	Differential lines	Yr Gene
YR10/ moro	Yr10	Moroco	Yr9 /Avocet	Yr9
Chines 166	Yr1	Australia	Haybrid 46	Yr4
YR15/Avocet	Yr15	Australia	Kalinsana	Yr7
YR18	Yr18	-	Lee	Yr7
Yr8/Avocet	Yr8+	Australia	Avocet r	Yr8

3.3.2 Fungal isolates

In this study, four isolates of *P. striiformis* from single spore were used. They were discovered in bread wheat leaf samples with stripe rust symptoms collected from naturally infected wheat fields in Ethiopia's main wheat-growing regions (Arsi and Bale areas). These isolates were obtained from the pathology laboratory at the Kulumsa Agricultural Research Centre (Table 6).

Table 6. Summary information of Ethiopian *P. striiformis* isolates used in physiological races analysis and efficacy test for Yr genes and wheat genotypes

<i>P. striiformis</i> Code	Isolate Name	Collection \ Zone	District	Geographic (UTM) ^a Longitude)	position (Latitude/	Altitude (masl)	Annual rainfall (mm)
I1	Deka	Arsi	Bekoji	39°10'E	7°35'N	2810	1020
I2	Hdasia	Arsi	Kulumsa	39°09'E	08001' N	2200	820
I3	Meraro	Arsi	Meraro	39°15'E	7°25'N	3007	1096
I4	Senatia	Bale	Sinana	40°10'E	7° 7'N,	2450	808

UTM^a =Universal Transverse Mercator coordinate system

3.3.3 Raising seedlings

Using artificial inoculation with known quantities of the fungal isolates, wheat genotypes grown in greenhouses were tested for the presence of race specific resistant genes. The experiment was carried out in the Plant Pathology Program greenhouse at Kulumsa Agricultural Research Centre. Each pot included five to six plants of the same wheat genotype were cultivated in 10 cm in diameter and 15 cm in depth plastic pots. The inoculated seedlings were incubated in a dew chamber with a relative humidity close to 100% and a mean temperature of about 18 °C for 24 hours. The plantlets were inoculated 14 days after planting, at the first leaf seedling stage. Clear plastic bags were placed over the seedlings to shield them from airborne pathogenic infection. To estimate resistant genes, ten differential lines with known Yr genes were also planted.

3.3.4 Inoculation of stripe rust monopustules

To evaluate the wheat genotypes and differential lines four stripe rust (*P. striiformis*) monopustules from Kulumsa Agricultural Research Centre were infected to 168 genotypes and 10 differential lines. These monopustules were collected from significant wheat-growing areas of Ethiopia's highlands (Table 5). A spore suspension was prepared at a concentration of 0.275 g/L (Negash et al., 2020). Plants on each plate were infected with spore suspensions of different isolates using a hand sprayer till run-off. For 96 hours, the inoculated seedlings were wrapped in aluminum foil and plastic bags to minimize cross contamination and to maintain a high humidity level for the establishment of infection.

3.3.5 Disease assessment

Stripe rust disease development was scored 14 to 15 days following inoculation. The yellow rust infection types (IT) experiment on test wheat genotypes was repeated. Seedling infection types were graded on 0-9 scale 14-15 days after inoculation based on the occurrence of necrosis, chlorosis, sporulation area size, and sporulation intensity (McNeal et al., 1971) (Table 7). Infection types (IT) 0-4 were thought to represent varied levels of incompatibility (host resistance and pathogen avirulence) between host and pathogen, whereas, infection types 5-6 were classified as intermediate responses. While, infection types 7-9 were thought to represent compatible (host susceptibility and pathogen virulence) relationships. The seedling response (RS) of each genotype to stripe rust infection was measured using the procedure outlined by Roelfs et al., (1992). Resistance genes were hypothesized by comparing the pathotypes low and high IT patterns on the tested entities to those of differential lines with known resistance genes. If a wheat variety exhibited a low or high IT pattern that matched a differential line with a known resistance profile, the tested genotype was thought to have the same resistance genes as the differential. This approach was applied sequentially to all Yr genes detected in the study of ten pathotypes.

Table 7. Major infection type classes for yellow rust

Infection type	Host response	Symptoms
0	Immune	No visible uredia
1	Very resistant	Minute necrotic flecks
2	Resistant	Necrotic areas without sporulation
3-4	Resistant to moderately resistant	Necrotic and chlorotic areas with restricted sporulation
5-6	Moderately resistant to moderately susceptible	Moderate sporulation with necrosis and Chlorosis
7	Moderately susceptible	Sporulation with chlorosis but no necrosis
8	Susceptible	Large uredia surrounded by chlorosis.
9	Very susceptible	Very large uredia with very little chlorosis

3.3.6 Data analysis

SAS version 9.4 (SAS, 2013) was used to perform an analysis of variance (ANOVA) for each isolate. To determine disease severity (DS) of each *P. striiformis* isolates, uredinia coverage were utilized (Kema et al., 1996). Seedling response (SR) on the other hand represents the response of the genotypes to the pathogen through host genotype interaction.

To rate disease severity and the seedling response on the tested wheat genotypes, five plants per isolate cultivar combination were visualized 14 days after inoculation. In addition, coefficient of infection (CI) was calculated by multiplying the stripe rust disease severity score (DS) by the seedling response values (SR = 0.0-0.8). Accordingly, bar graphs of the DS and SR 178 genotypes were generated with the help of ggplot2 (Wickham, 2016) and ggpubr (Kassambara, 2023) software packages. For disease severity, genotypes were categorized as immune (DS=0), resistant ($0 < DS \leq 3$), intermediate ($3 < DS \leq 6$), and susceptible ($6 < DS \leq 9$). Similar classifications were made for the 178 Genotypes seedling that responded to each Pst isolates as: immune (PR=0), resistant ($0 < SR \leq 0.2$), intermediate ($0.2 < SR \leq 0.8$), and susceptible ($0.8 < SR \leq 1$) (Supplementary Table 2). These bread wheat genotypes were also categorized according to their coefficient of infection as immune (PR=0), resistant ($0 < CI \leq 2$), intermediate ($2 < CI \leq 4.8$), and susceptible ($4.8 < C \leq 19$) to each Pst isolates (Line et al., 1992; Liu et al., 2017). To expose the genotype-by-isolate interaction, mean coefficients of infection values were subjected to hierarchical cluster analysis (Supplementary Table 3). Cluster analysis was carried out in R programing software using the ggplot2 (Wickham, 2016) and factoextra (Alboukadel and Fabian, 2020) packages.

3.4 Genetic architecture of adult-plant stripe rust resistance in bread wheat genotypes association Panel; GWAS

3.4.1 Plant materials and evaluation of stripe rust resistance in adult plants

A total of 178 bread wheat genotypes (including 165 recombinant inbred lines received from the International Maize and Wheat Improvement Center (CIMMYT) and 13 commercial cultivars cultivated in Ethiopia) were used in the current study (genotypes in Table 3 except genotypes 9 and 95). The genotypes from CIMMYT were comprised of six genotypes from the National Variety Trial, five from the Adaptation Trial, 34 from the High Rain Wheat Screening Nursery, 49 from the International Bread Wheat Screening Nursery, 53 from the International Septoria Observation Nursery, 14 from the High Rain Wheat Yield Trial, and the remaining three genotypes were from preliminary variety trial. The bread wheat genotypes were evaluated across three locations, namely, Kulumsa Agricultural Research Centre (KARC) ($8^{\circ} 02' N / 39^{\circ} 15' E$), Meraro (substation of KARC)

(07° 24' 27' N/ 39° 14' E), and Holeta Agricultural Research Centre (HARC) (9° 3' N/38° 30' E) in the 2020/21 main cropping season. The wheat genotype Kingbird (G40) was used as the standard check in the field evaluation. The experiment was set up using an alpha-lattice design with two replications, six sub-blocks, and 30 entries per sub-block per replication, with two rows per entry (Supplementary Table 1). Each accession was sowed manually at 1m length, 0.20 m spacing between rows, and 0.4 m between entries. Spaces between blocks and replications were maintained at a 1.50 m distance. All trials were seeded with 150 kg of seeds per hectare, fertilized with 100 and 75 kg of N and P₂O₅ each, and weeded three times by hand-picking. To provide enough disease pressure, the sensitive cultivar "Morocco" was sown as a diffuser row throughout the length of the blocks.

The modified Cobb scale (Peterson et al., 1948) was used to measure the disease severity (DS), with values ranging from 0% to 90%. Moreover, the genotypes' field response (FR) to stripe rust infection was scored following the procedure described by Roelfs, et al., (1992) as Immune = no uredinia or other macroscopic sign of infection; R = resistant, small uredinia surrounded by necrosis; MR = moderately resistant, medium to large uredinia surrounded by necrosis; MRMS=moderately resistant to moderately susceptible; MS = moderately susceptible, medium to large uredinia surrounded by chlorosis; or S = susceptible, large uredinia without necrosis or chlorosis. For statistical analysis, each replicate's genotype responses for immune, resistant, moderately resistant, moderately resistant to moderately susceptible, moderately susceptible, and susceptible were translated into the values 0, 0.2, 0.4, 0.6, 0.8, and 1, respectively (Elbasyoni et al., 2019). When the disease severity was greater than or equal to 50% and a susceptible reaction (S) was seen on the spreader rows, the plant resistance response was scored, and this resulted in a combined value of 50S (Alemu et al., 2021).

In addition to the disease data, important agronomic traits such as days to 50% heading (HD), days to 50% flowering (FD), days to maturity (MD), thousand kernel weight (TKW), grain yield per plot (GYPP), plant height (PH), spike length (SL), flag leaf area (LA), number of spikelets per spike (NSsS), number of kernels per spike (NKS), number of kernels per spike (NKS), and spike weight (SW) were recorded. Days to heading, flowering, and maturity were recorded for whole plots when 50% of the plants reached the

corresponding Zadock's growth stages. Plant height and spike length were measured at the physiological maturity stage in five randomly selected and tagged plants. Data on the number of spikelets per spike, the number of kernels per spikelet, and the total number of kernels per spike were determined from the five randomly tagged plants per entry per replication by collecting their spikes separately.

3.4.2 Data analysis

3.4.2.1 Phenotype data analysis

The coefficient of infection (CI), which indicates the combined reaction of the genotypes for the disease, was created by multiplying the disease severity score (DS=0 - 90) by the genotype field response values (FR=0.0 - 1). An analysis of variance (ANOVA) for each and combined environments was carried out using SAS version 9.4 (SAS, 2013) based on a linear mixed model (LMM). In the analysis of variance for individual environments, genotype and the incomplete block were considered as fixed and random factors, respectively, to compute the ANOVA for each location. The observed phenotypic response of the i^{th} genotype in the j^{th} replication and the l^{th} sub-block was calculated for an individual environment using the following model:

$$y_{ijl} = \mu + g_i + \gamma_j + bl_{(j)} + \varepsilon_{ij} \quad (8)$$

Where, y_{ijl} = measured phenotype, g_i = fixed effect of the i^{th} genotype, μ = grand mean, γ_j = effect of the j^{th} replication, $bl_{(j)}$ = random effect of the i^{th} block nested within the j^{th} replication, and ε_{ijl} = random error term.

Combined ANOVA was calculated by treating the genotype as a fixed variable and the incomplete block and location as random effects as LMM:

$$Y_{jklm} = \mu + g_m + \gamma_{jk} + e_j + b_{jkl} + (ge)_{jm} + \varepsilon_{jklm} \quad (9)$$

where Y_{jklm} = observed response of genotype m , replication k of block l at location j ; b_{jkl} = random effect of block l nested with replication k in location j and is $\sim \text{NID}(0, \delta_b^2)$; g_m = fixed effect of genotype m ; μ = grand mean; r_{jk} = effect of replication k in location j ; e_j = random effect of location j and is $\sim \text{NID}(0, \delta_e^2)$; $(ge)_{jm}$ = random effect of the interaction

between genotype m and location j and is $\sim \text{NID}(0, \delta_{ge}^2)$; and ε_{jklm} = random residual effect and $\sim \text{NID}(0, \delta_{\varepsilon}^2)$. Variance components were computed.

The genotypes were classified into resistant, intermediate, and susceptible groups based on the average values of DS, FR, and CI for the pooled data from all environments at each growth stage. Bar plots showing DS, FR, and CI of the 178 genotypes were plotted using the ggplot2 (Wickham, 2016) and ggpubr (Kassambara, 2023) packages in R software (R Core Team, 2020). The yellow rust resistance traits' broad sense heritability (H^2) at the environmental level was calculated through an analysis of variance using the following formula:

$$H^2 = \frac{\delta^2 g}{\delta^2 g + \delta^2 \varepsilon / r} \quad (10)$$

Broad-sense heritability across environments was predicted by the formula:

$$H^2 = \frac{\delta^2 g}{\delta^2 g + \delta^2 ge / l + \delta^2 \varepsilon / lr} \quad (11)$$

where, $\delta^2 g$ is the genotypic variance, $\delta^2 ge$ is the genotype-by-location interaction variance, $\delta^2 e$ is the location variance, and l and r represent the numbers of locations and replicates, respectively. The virility package in the R for Windows Version 4.2.3 program was used to analyze the correlation analysis between the various parameters (Raj et al., 2020).

3.4.2.2 Genomic DNA extraction and genotyping-by-sequencing

For genomic DNA extraction, the study wheat plants were grown in greenhouse conditions at the National Agricultural Biotechnology Research Center (NABRC), Holeta, 29 km west of Addis Ababa. Leaves from 2-week-old seedling were collected into 96 well samples collecting plates and dried at 50°C overnight. The leaf samples were sent to BecA-ILRI, Hub laboratory in Nairobi, Kenya for SNP genotyping using Diversity Arrays Technology sequencing (DArTseqTM technology) with the support of the Integrated Genotyping Service and Support (IGSS) program. Genomic DNA was extracted using a Nucleomag Plant Genomic DNA extraction kit (MACHEREY-NAGEL GmbH & Co. KG, Germany) according to the manufacturer's instruction. DNA quality and quantity were assessed using a Nanodrop spectrophotometer (thermo scientificTM nanodropTM lite plus microvolume

spectrophotometer) and 1% agarose gel electrophoresis, respectively. SNP genotyping was done by utilizing GBS technology, using an Illumina HiSeq2500 following the procedure described by Elshire, et al., (2011). Genome complexity reduction was carried out by digesting genomic DNA with ApeKI, a type II restriction endonuclease that recognizes a degenerate 5-bp sequence (GCWGC, where W is A or T). For genotyping, the library was constructed by ligating common and barcode adaptors to the sticky ends of each fragment. The adapter-ligated fragments were PCR amplified, and then sequenced by synthesis using single-read sequencing runs for 77 bases. Next-generation sequencing of the GBS library was carried out using an Illumina HiSeq2500 lane following the manufacturer's protocol.

3.4.2.3 Quality control and SNP calling

Based on alignment with the reference genome of Chinese Spring Wheat RefSeq v1.0 (IWGSC, 2018), the DArTSeq SNP markers were scored using the DArTsoft14 software implemented in the KDCompute plug-in system created by Diversity Arrays Technology (<https://kdcompute.seqart.net/kdcompute/login>). SilicoDArT and SNP markers, which were both scored in binary ways (1/0), reflect the existence or absence of marker data in the genomic representation of each sample (Akbari et al., 2006). Marker quality control was maintained by filtering or removing mono-morphic -markers, markers with lower call rates (>30% missing), and markers with minor allele frequencies (MAF <5%). Genotypes with >30% missing marker data were also removed from the analysis.

3.4.2.4 Population structure analysis

Bayesian model-based clustering in STRUCTURE software version 2.3.4 was used to determine the population admixture pattern (Pritchard et al., 2000). The STRUCTURE program was run with the admixture model, correlated allele frequencies, a burn-in period of 10,000, and 50,000 Markov Chain Monte Carlo (MCMC) replications after burn-in for the hypothetical sub-population K from 1 to 10 with 10 iterations. The STRUCTURE HARVESTER was used to determine the optimum K value, according to Evanno et al., (2005). The clumpak beta version was used to determine the bar graph for the ideal K (Kopelman et al., 2015). Principal component analysis (PCA) was computed using GAPIT software to determine the population spatial distribution and clustering.

3.4.2.5 Genome-wide association study

GAPIT software was used to conduct a marker-trait association analysis (Lipka et al., 2012). GWAS was carried out for the coefficient of infection at five growth stages, including yellow rust resistance at pre-heading (YRPH), yellow rust resistance at heading (YRH), yellow rust resistance at flowering (YRF), yellow rust resistance at mid-maturity (YRMM), and yellow rust resistance at maturity (YRM), and some significant agro-morphological traits such as days to 50% (FD), days to 90% maturity (MD), leaf area (LA), plant height (PH), number of kernels per spike (NKS), thousand-kernel weight (TKW), and grain yield (GY) in each individual environment and across all environments. The marker-trait association analysis involved a total of 6,788 robust SNPs with a call rate > 70% and MAF > 5%. Missing SNPs were imputed using optimal impute ver. 1.0.0 based on the KNN imputation method in the KDcompute_plugin system. The LD measure r^2 ver.0.2.2 in KDcompute_plugin system was used to determine marker distribution on individual chromosomes.

TASSEL Ver. 5 (Bradbury et al., 2007) was used to calculate the pairwise LD measurements (r^2 and p -value) between markers on each chromosome. A genome-wide scale LD decay scatter plot was produced by plotting r^2 values against physical distance (bp) using GAPIT software. An $r^2 = 0.2$ was used as a cut-off to declare no LD between pairs of markers. The confidence range for establishing a discrete QTL for each chromosome was calculated using the physical distance at which the LD declined to the crucial $r^2 = 0.2$. If the distance between the significant SNP markers was smaller than the critical physical distance, they were assigned to the same QTL if they were on the same chromosome.

Bayesian information and Linkage-disequilibrium Iteratively Nested Keyway (BLINK) model, implemented in the GAPIT R package (Tang et al., 2016), was used to conduct GWAS. BLINK was selected because of its high computing efficiency and statistical power to control spurious associations due to population structure and kinship. BLINK presented the best Bayesian information criterion value for across and individual environments. Kinship (K) matrix was computed using Van-Raden (2008) method. The model's fitness to control population structure and familial relatedness of the study samples was examined by

observing using the quantile-quantile (QQ) plot created from $-\log_{10} p\text{-values}$. Marker-trait associations (MTAs) were considered to be significant when they surpassed the significant threshold of the nominal p-values of 0.001 or $-\log_{10} (p\text{-values}) = 3$. Manhattan plot and Q-Q were observed using the R package qqman (Turner, 2014) to identify significant MTAs. Furthermore, candidate genes in the detected significant regions were annotated MTAs from the recently released IWGSC RefSeq Annotation v2.1 available at <https://wheat-urgi.versailles.inrae.fr/SeqRepository/Annotations>.

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 Genetic diversity and population structure analysis of bread wheat genotypes as revealed by ISSR markers

4.1.1 Result

4.1.1.1 ISSR primers and their banding patterns

Among the tested ISSR markers, 10 primers amplified fragments ranging from 200 to 2,600 bp that were relatively highly polymorphic, and reproducible with clear bands and an unambiguous amplification (Figure 9), generated a total of 166 bands (Table 8,). Figure 9 presents a sample of scoreable polymorphic bands that were generated by primer UBC 834. The number of scorable bands for individual primers ranged from 12 to 25, with an average number of bands of 16.6 per primer. The highest number of bands was generated by primer UBC 873 with 25 bands, followed by primer UBC 834 with 21 bands. Whereas, the lowest amplification was recorded for primer 844, which generated 12 bands (Table 8). The fragment size amplified with these primers ranged from 150 to 1600 bps. The 10 primers were composed of di- and tetra-nucleotide sequences, and those with dinucleotide motifs (AG)_n and (CT)_n produced a high level of polymorphism.

Table 8. Reproducible and polymorphic ISSR primers with their primer motif, annealing temperature (°C), amplification patterns, fragment size and scorable bands

Primer	Primer motif	Annealing temperature °C	Amplification pattern	Fragment Size (bp)	Scorable bands
UBC 822	(AC)8T	49	Reproducible & Polymorphic	500-1500	13
UBC 825	(AC)7T	48	Reproducible & Polymorphic	200-1400	14
UBC 826	(AC)8C	52	Reproducible & Polymorphic	150-2000	13
UBC 834	(AG)8GTT	52	Reproducible & Polymorphic	200-2100	21
UBC 836	(AG)8GTA	49	Reproducible & Polymorphic	150-1400	20
UBC 844	(CT)8RC	48	Reproducible & Polymorphic	400-2600	12
UBC 848	(CA)8NG	48	Reproducible & Polymorphic	200-2100	14
UBC 853	(TC)8RT	49	Reproducible & Polymorphic	350-2500	13
UBC 857	(AC)8YG	52	Reproducible & Polymorphic	300-2000	21
UBC 873	(GACA)4	45	Reproducible & Polymorphic	150-1900	25

N : (A, T, G, C); R : (A, G); Y : (C, T)

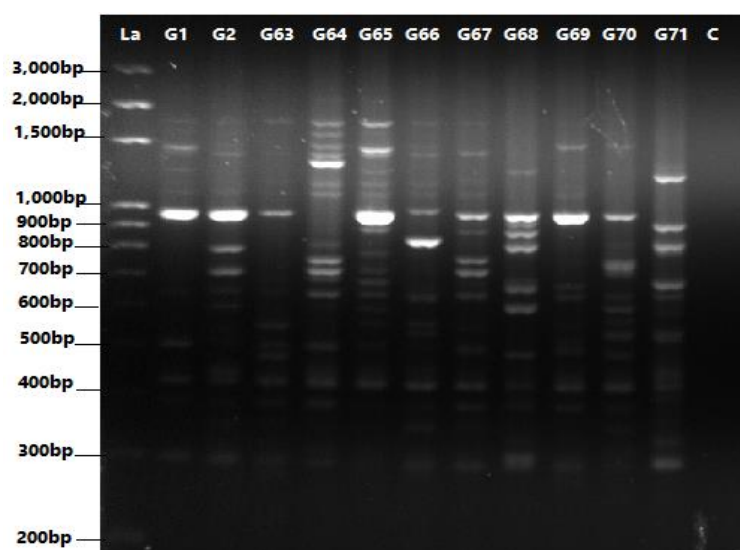


Figure 9. Banding pattern of ISSR primer UBC 834 in 11 bread wheat genotypes (La: DNA ladder, G=genotype and the numbers denote the codes of the 11 wheat genotypes used, and C=negative control).

4.1.1.2 ISSR based genetic diversity in bread wheat genotypes

The analysis revealed that the ISSR markers used were highly polymorphic and informative with a mean number of alleles of 1.90 (range 1.62 – 2.00), effective number of alleles of 1.43 (range 1.05-1.78), Shannon's Information index of 0.26 (range 0.04-0.42), Nei's gene diversity of 0.40 (range 0.09-0.61), and gene flow of 5.34 (range 2.02 – 14.64). The highest number of allele ($N_a=2.00$), effective number of allele ($N_e=1.78$), gene diversity ($h=0.61$

and Shannon's information index ($I=0.42$) were obtained for primer 834, while primer UBC-853 resulted in least values for the corresponding genetic diversity indices. The maximum percentage of polymorphic loci (100%) was produced by UBC-834, followed by UBC-857 (90.5%). However, primers UBC-826 and UBC-853 generated the least percentage of polymorphic loci, accounting for 61.5% and 50.0%, respectively. The locus polymorphic information content ranged from 0.34 (UBC-853) to 0.43 (UBC-834) with an overall mean value of 0.21. Markers with a PIC value between 0.25 and 0.5 were considered moderately informative, and less than 0.25 were considered less informative. Accordingly, 40% of the used ISSR markers showed moderate PIC (Table 9). Likewise, 50% of the primers (5) demonstrated PIC values greater than the average value (0.21).

Table 9. Informativeness and other genetic diversity summary statistics of all ISSR loci

Primer	Na	Ne	I	H	H _T	H _S	Gst	Nm	PPL	PIC
UBC 822	1.85	1.34	0.22	0.34	0.16	0.15	-0.45	7.98	84.6%	0.14
UBC 825	2.00	1.27	0.20	0.35	0.17	0.14	0.15	3.24	85.7%	0.13
UBC 826	2.00	1.27	0.20	0.35	0.17	0.14	0.15	3.24	61.5%	0.13
UBC 834	2.00	1.78	0.42	0.61	0.44	0.36	0.17	6.06	100%	0.43
UBC 836	1.95	1.50	0.29	0.44	0.28	0.21	0.21	3.43	90%	0.26
UBC 844	1.83	1.50	0.29	0.43	0.22	0.18	0.17	4.83	83.3%	0.22
UBC 848	2.00	1.60	0.36	0.54	0.34	0.26	0.21	2.02	71.4%	0.29
UBC 853	1.62	1.05	0.04	0.09	0.04	0.04	0.08	14.67	53.8%	0.07
UBC 857	1.95	1.50	0.29	0.44	0.28	0.21	0.21	3.43	90.5%	0.13
UBC 873	1.84	1.47	0.28	0.43	0.29	0.24	0.23	4.52	84%	0.34
Mean	1.90	1.43	0.26	0.40	0.24	0.19	0.11	5.34	80.5%	0.21

Na : Observed number of alleles; Ne : Effective number of alleles; I :Shannon's Information index; H: Nei's gene diversity; H_T :Total genetic diversity H_S : genetic differentiation; Gst: Genetic differentiation statistics by locus; Nm : estimate of the number of migrants (gene flow) from Gst where $Nm = 0.5(1 - Gst)/Gst$, PPL : Percent of polymorphic Loci and PIC: polymorphic information content.

4.1.1.3 Genetic variability within and among populations

The average within population genetic diversity estimates for the varying population sizes ranging from 3-56 were: estimated allele frequency (p and q), p of 0.54 and q of 0.46, observed alleles of 1.47, effective alleles of 1.33, Shannon's information index of 0.29, Nei's gene diversity value of 0.19, unbiased expected heterozygosity of 0.20 and percentage of polymorphic loci of 65.06%. The ISEPTON population showed the highest observed

number of alleles, effective number of alleles, Nei's gene diversity, Shannon's information index, and PPL while IBWSN and HRWSN populations ranked second and third, respectively. The highest and the lowest Nei's gene diversity were observed in the populations of ISEPTON and PVT, respectively. Fifty percent of the studied populations displayed a genetic diversity greater than mean value ($h = 0.19$) and the PPL per population was between 15.06% (PVT) and 83.13% (ISEPTON) with an overall mean of 57.23%. A summary of the different genetic diversity estimates over all loci across populations is presented in Table 10.

Table 10. Allelic patterns and diversity indices across eight wheat populations estimated from 10 ISSR markers

Population	N	Band frequency	p	q	Na	Ne	I	h	uHe	PPL (%)
DAT	5	0.65	0.62	0.38	0.87	1.10	0.08	0.06	0.06	15.06
COV	13	0.64	0.54	0.46	1.34	1.33	0.28	0.19	0.20	51.20
HRWSN	34	0.62	0.51	0.49	1.60	1.39	0.33	0.22	0.23	65.66
HRWYT	14	0.62	0.49	0.51	1.78	1.43	0.38	0.25	0.26	78.92
IBWSN	49	0.62	0.50	0.50	1.77	1.41	0.38	0.25	0.25	78.92
ISEPTON	56	0.63	0.50	0.50	1.82	1.44	0.40	0.26	0.27	83.13
NVT	6	0.67	0.58	0.43	1.41	1.32	0.27	0.184	0.20	50.00
PVT	3	0.66	0.59	0.41	1.18	1.24	0.20	0.138	0.17	34.94
Mean	22	0.64	0.54	0.46	1.47	1.33	0.29	0.19	0.20	57.23

N: sample size, Na: Observed number of alleles, p & q: Estimated Allele Frequency, Ne: Effective number of alleles, h: Nei's gene diversity, I: Shannon's Information index uHe: Expected and Unbiased Expected Heterozygosity and PPL: percentage of polymorphic loci. Na : No. of Different Alleles, Ne : No. of Effective Alleles : $1 / (p^2 + q^2)$, I : Shannon's Information Index : $-1 * (p * \ln(p) + q * \ln(q))$, He = Expected Heterozygosity : $2 * p * q$, uHe : Unbiased Expected Heterozygosity : $(2N / (2N-1)) * He$ Where for Diploid Binary data and assuming Hardy-Weinberg Equilibrium, $q : (1 - \text{Band Freq.})^{0.5}$ and $p : 1 - q$. Population abbreviations are: ADT : Adaptation Trial, COV : Commercial varieties, HRWSN : High rain weed trial screening nursery, HRWYT : High rain weed yield trial, IBWSN : International bread wheat screening nursery, ISEPTON : International Septoria observation nursery, NVT : National Variety trial and PVT : Primary Variety trial.

4.1.1.4 Banding patterns across populations

In the banding pattern analysis of 180 genotypes that were grouped into eight populations, HRWSN represented the highest number of bands (165), followed by ISEPTON and IBWSN with 164 and 163 bands, respectively, while ADT comprised the lowest number of bands (120). The highest mean heterogeneity (0.19) was observed in COV, followed by

NVT and PVT with mean heterogeneities of 0.18 and 0.14, respectively. Private bands used for distinguishing populations from each other were not identified, i.e., all populations had no private band (Figure 10).

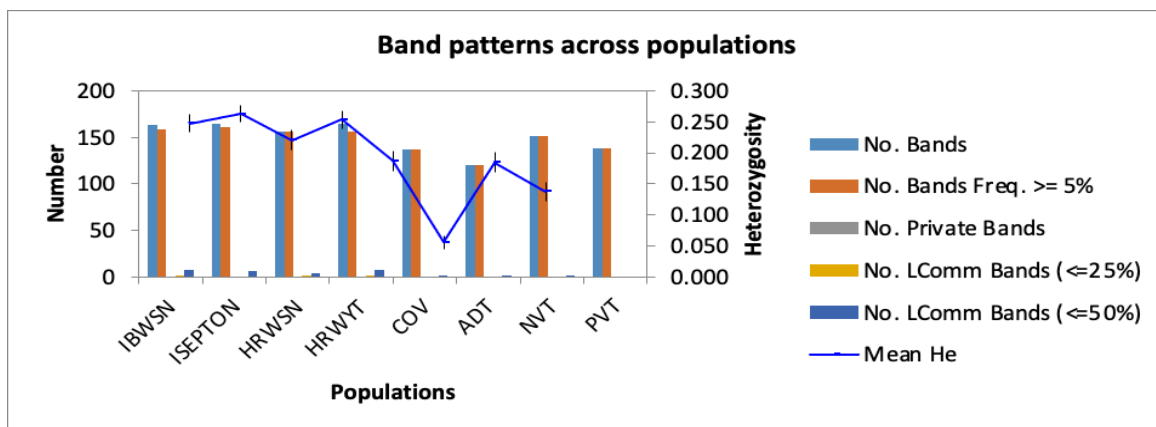


Figure 10. Band pattern across populations, Population abbreviations are ADT = Adaptation Trial, COV = Commercial varieties, HRWSN = High rain weed trial screening nursery, HRWYT = High rain weed yield trial, IBWSN = International bread wheat screening nursery, ISEPTON = International Septoria observation nursery, NVT = National Variety trial and PVT = Primary Variety trial.

4.1.1.5 Genetic relationships among the populations

Estimates using genetic distance (below diagonal) showed the highest genetic distance of 0.14, 0.12, and 0.1 between the populations of PVT and COV, PVT and DAT, and HRWSN and PVT, respectively. A low genetic distance (0.01) was observed between the populations of IBWSN and HRWSN (Table 11).

Table 11. Pairwise Nei's measures of genetic distance

Pop ID	DAT	COV	HRWSN	HRWYT	IBWSN	ISEPTON	NVT	PVT
DAT	****							
COV	0.06	****						
HRWSN	0.05	0.03	****					
HRWYT	0.07	0.05	0.02	****				
IBWSN	0.05	0.03	0.01	0.02	****			
ISEPTON	0.06	0.03	0.01	0.02	0.01	****		
NVT	0.07	0.06	0.04	0.04	0.05	0.05	****	
PVT	0.12	0.14	0.10	0.09	0.03	0.09	0.09	****

Population abbreviations are: ADT = Adaptation Trial, COV = Commercial varieties, HRWSN = High rain weed trial screening nursery, HRWYT = High rain weed yield trial, IBWSN =

International bread wheat screening nursery, ISEPTON = International Septoria observation nursery, NVT = National Variety trial and PVT = Primary Variety trial.

The pairwise coefficient of genetic differentiation between the populations ranged from 0.000 (PVT and NVT) to 0.410 (between PVT and DAT). The highest and statistically significant genetic differentiation, ($\Phi_{IT} = 0.410$, $p = 0.017$) was observed between populations of PVT, and DAT, implying the lowest gene flow between them. The second-highest genetic differentiation with a gene flow rate of 0.352 was observed between the populations of NVT and HRWYT. The genetic differences between populations of HRWYT and IBWSN, NVT and PVT, HRWYT and NVT, ISEPTON and PVT, HRWSN and PVT, ISEPTON and NVT, ISEPTON and NVT, HRWYT and ISEPTON, COV and HRWS, and IBWSN and PVT were not statistically significant ($p > 0.05$) (Table 12).

Table 12. Population genetic differentiation measured by Φ_{IT} (below the diagonal) between the eight bread wheat populations with p-values above the diagonal

Pop ID	DAT	COV	HRWSN	HRWYT	IBWSN	ISEPTON	NVT	PVT
DAT	****	0.036	0.003	0.001	0.001	0.001	0.006	0.017
COV	0.118	****	0.123	0.001	0.001	0.001	0.001	0.024
HRWSN	0.183	0.029	****	0.001	0.001	0.012	0.015	0.304
HRWYT	0.257	0.166	0.082	****	0.406	0.200	0.352	0.272
IBWSN	0.233	0.140	0.078	0.000	****	0.168	0.200	0.100
ISEPTON	0.174	0.107	0.043	0.006	0.006	****	0.213	0.269
NVT	0.365	0.204	0.104	0.005	0.019	0.021	****	0.388
PVT	0.410	0.173	0.024	0.024	0.061	0.028	0.000	****

4.1.1.6 Genetic relationship within and among populations

An analysis of molecular variance (AMOVA) was performed to observe variation among and within-populations. Analysis of molecular variance using the 166 ISSR bands generated by the ten primers in eight bread wheat populations revealed that a higher percent (95%) of the total genetic variation was attributed to within-population leaving only 5% for among-populations genetic variability. The populations showed statistically significant low genetic differentiation (F_{ST} value of = 0.054; $p < 0.001$). The AMOVA results revealed highly significant genetic differences ($p < 0.001$) among the eight bread wheat populations (Table 13).

Table 13. Analysis of molecular variance (AMOVA) within and among populations

Source of variation	Df	SS	MS	Est. Var.	PV	FST	P-value
Among Pops	7	317.93	45.42	1.21	5%	0.05	P<0.001
Within Pops	172	3640.34	21.17	21.17	95%		P<0.001
Total	179	3958.26		22.37	100%		

d.f = Degree of freedom, S.S = Sum of squares, MS = Mean square, Est. Var. = Estimated Variation, PV = Percent of variation and FST = Fixation indices

4.1.1.7 Cluster analysis using PCoA and UPGMA

Principal Coordinate Analysis (PCoA) is a technique frequently used in multivariate statistics to display the pattern of genetic structure and similarly to determine the amounts of variance described per component and cumulatively (Mekonnen et al., 2020). In the current research, PCoA explained 34.46% of the total genetic variations, and the first three axes (1, 2, and 3) accounted for 19.63%, 14.83%, and 9.29%, respectively. It clustered the entire population into three subgroups with high genetic admixture. PCoA clustered the ADT, COV, and NVT populations together. However, individuals from HRWYT, IBWSN, and ISEPTION populations showed a nearly uniform distribution on the two-dimensional coordinate plane without distinct population clustering. None of the clusters were composed entirely of genotypes from a particular population (Figure 11).

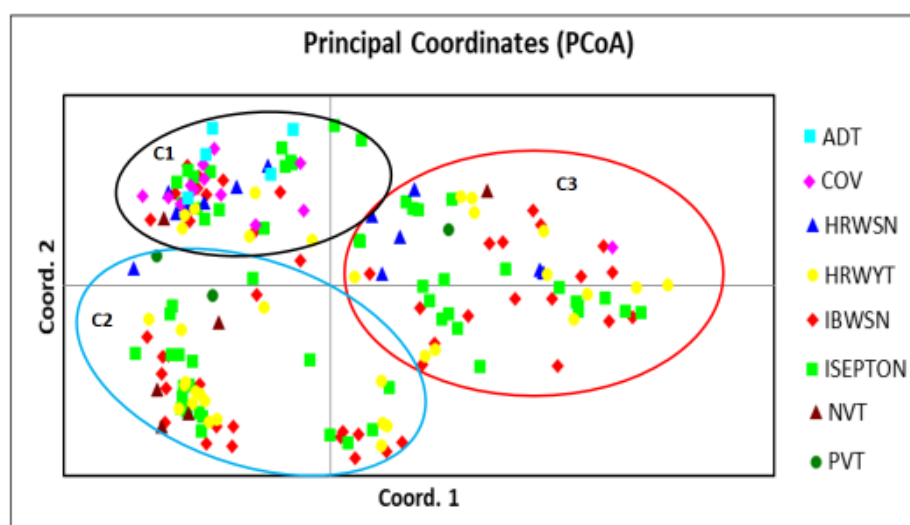


Figure 11. PCoA of the 180 bread wheat genotypes as revealed by 10 ISSR markers, Samples coded with the same symbol and color belongs to the same population. Population abbreviations are: ADT: Adaptation Trial, COV: Commercial cultivars, HRWSN: High rain weed trial screening nursery, HRWYT: High rain weed yield trial, IBWSN: International bread wheat screening nursery,

ISEPTON: International Septoria observation nursery, NVT: National variety trial and PVT: Primary variety trial

The dendrogram generated using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) grouped the eight populations into three major clusters (C1, C2, and C3), each of which was further grouped into two sub-clusters. One hundred eighteen (66%) of the genotypes were assigned to C3 followed by C2, which were composed of 38 (21%) individuals. The lowest numbers 24 (13%) of germplasm were assigned to cluster C2 (Figure 12). None of the major clusters were composed of individuals from a single population, indicating the presence of high genetic admixture. The dendrogram generated using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) also grouped the eight populations into three major clusters (Figure 12).

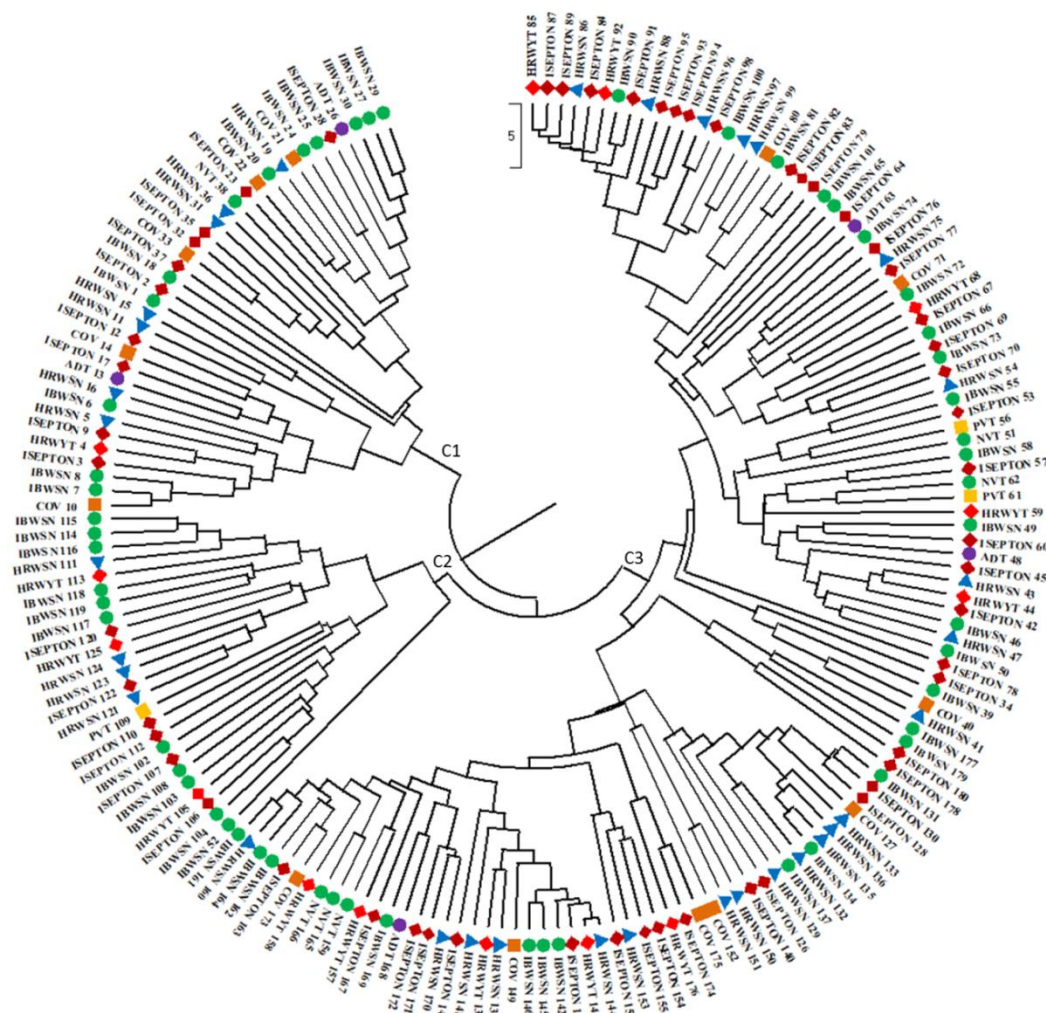
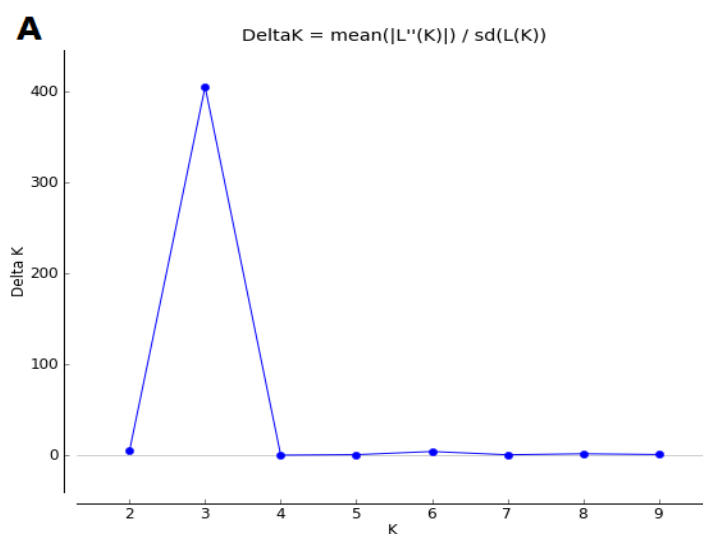


Figure 12. The UPGMA based clustering of 180 bread wheat from the eight populations, Samples coded with the same symbol and color belongs to the same population. Population abbreviations are: ADT: Adaptation Trial, COV: Commercial varieties, HRWSN: High rain weed trial screening nursery, HRWYT: High rain weed yield trial, IBWSN: International bread wheat screening nursery, ISEPTON: International Septoria observation nursery, NVT: National variety trial and PVT: Primary variety trial.

4.1.1.8 Population genetic structure analysis

It is known that testing for population structure is important while conducting association investigations and drawing relationships between markers. Accordingly, wheat germplasm can be efficiently categorized using population structure analyses, and maximum membership probability in STRUCTURE. The UPGMA clustering and PCoA group the wheat populations in two three clusters, indicating the presence of mixing of genetic material among the eight populations. The Bayesian model-based population structure of the 180 wheat genotypes was applied using Structure v2.3.4 software, and the K value was used to estimate the number of clusters of the isolates. The output of the structure harvester revealed that the delta K (ΔK) values reached a sharp peak at K = 3 (Figure 13A). The Clumpak result (bar plot) also detected a combination of traits from multiple ancestral groups between the three subpopulations (Figure 13B). The rationale and significance of the grouping of genotypes are to better understand the genetic diversity within a population and to identify potential relationships between certain traits. This information can be crucial for breeding programs, conservation efforts, and understanding evolutionary processes.



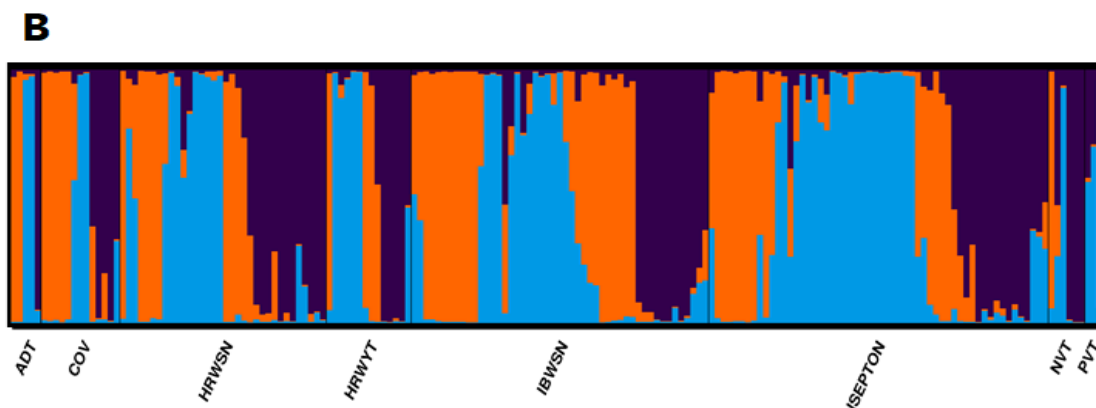


Figure 13. Population structure analysis of 180 bread wheat genotypes, (A) Best estimated delta K value and (B) Estimated population structure for K = 3. The blue, orange and black colours represent genetic groups designated by Structure Harvester. Population abbreviations are: ADT: Adaptation Trial, COV: Commercial varieties, HRWSN: High rain weed trial screening nursery, HRWYT: High rain weed yield trial, IBWSN: International bread wheat screening nursery, ISEPTON: International Septoria observation nursery, NVT: National variety trial and PVT: Primary variety trial.

4.1.2 Discussion

Genetic diversity in wheat has been increasingly narrowed down due to different factors (Apoorva et al., 2014). Besides, for the improvement of existing germplasm genetic diversity investigations are important (Zeb et al., 2009). In the current research, the genetic diversity and population structure analysis of 180 bread wheat genotypes were conducted so that they could be used in the selection of parents with desirable traits for forthcoming breeding programs and also for sustainable use of this valuable genetic resource.

4.1.2.1 Polymorphism level of the ISSR markers

In this study, ISSR primers with dinucleotide motifs (AG)_n and (CT)_n produced a high level of polymorphism in bread wheat, indicating these markers are suitable for studying genetic variation. The result is in agreement with other investigations (Carvalho et al., 2009; Najaphy et al., 2011). In this research, of the total 166 DNA fragments (bands) produced, 134 (80.5%) fragments were polymorphic, and the polymorphism among genotypes ranged from 53.8 to 100% with an average of 80.5%, and the mean number of bands per primer was 16.6. This polymorphism among genotypes was in line with Ateş-Sönmezoglu et al., (2022), which was 75%. The total number of bands observed in this research was substantially higher than reported by Abdollah et al., (2011) who reported a

total of 86 bands, with the percentage of polymorphic bands ranging between 60 and 100 and an average of 80.2% using 10 ISSR primers. The mean number of bands per locus observed in the present research (16.6) was considerably higher than the level (8.6 bands per primer) reported by Abdollah et al., (2011). The difference is attributed to the high number of genotypes used in the present research, marker polymorphism differences, and also genotype variations.

In this study, the polymorphic information content of the used ISSR loci was found across populations ranging from 0.07 to 0.43, with an overall mean of 0.21. On the other hand, Ateş-Sönmezoğlu et al., (2022) reported a 0.55 mean PIC, which is much higher than the mean PIC investigated in this study. This could be likely due to PIC observed in most of the ISSR primers could be attributed to the diverse nature of the bread wheat germplasm and/or the highly informativeness of the ISSR markers used.

4.1.2.2. Population genetic diversity

Worldwide, wheat production is facing challenges due to the impact of abiotic and biotic stresses. Consequently, it is important to look for germplasm with the highest genetic diversity of important traits through research for effective conservation and improvement of existing germplasm. Wheat genotypes are thus used in many wheat breeding programs because they have a unique potential and diversity of essential genes that influence both biotic and abiotic stressors (Manickavelu et al., 2016; Tehseen et al., 2022). It could be useful for exploring genetic constituents and identifying loci, which are then used to improve wheat performance in breeding programs. In the present research genetic diversity in the studied wheat populations was determined, and gene diversity and Shannon's information index were found to be 0.19 and 0.29, respectively. The levels of gene diversity and Shannon's information index obtained in the current research differed from those reported by (Abouized et al., 2013), most likely due to substantial gene flow, which reduced the amount of variation among groups. The average genetic diversity across populations observed in the present research was in agreement to the level reported by Fatih et al., (2022), which was 0.33. In line with this, Abou et al. (2013) and Abdel and Hewedy (2018) reported that ISSR markers are highly efficient in discriminating wheat genotypes. The observed population genetic diversity in this research was consistent with Haliloglu et

al., (2023) results for gene diversity (0.095) and Shannon's information index (0.114). Among the eight studied wheat populations, the ISEPTON population showed the highest observed number of alleles ($N_a = 1.82$), effective number of alleles ($N_e = 1.44$), Nei's gene diversity ($h = 0.26$), Shannon's information index ($I = 0.40$) and PPL (83.13%). This could likely be due to its highest population size as compared to the other populations. This implies that ISEPTON populations could be a good source of valuable alleles for wheat improvement as compared to the other populations.

4.1.2.3 Population genetic structure

Analysis of molecular variance (AMOVA) revealed a higher (95%) genetic diversity within the population than among populations (5%), likely due to high gene flow among populations. Similarly, higher genetic diversity within populations was reported by Sofalian et al., (2008). The high gene flow ($N_m = 5.34$) could be attributed to the genetic diversity differences. Basically, a high level of genetic differentiation among populations is inversely proportional to gene flow (Wang et al., 2012; Dalvand et al., 2018). Genetic diversity is considerably influenced by gene flow. Pollen movement among populations, seed exchange practices between communities, and common marketing as well as socio-economic conditions may have facilitated the high gene flow ($N_m = 5.34$) among populations, leading to lower among-population genetic differentiation (F_{st} : 0.05).

Principal coordinate analysis and UPGMA also confirmed the presence of higher genetic variation at the population level than among populations. PCoA resulted in three clusters, where none of the clusters were composed of germplasm entirely from a particular population. This implies the existence of a significant intermixing of genetic backgrounds among the populations. Likewise, STRUCTURE analysis supported PCoA, and signifying the presence of high genetic relationships among the studied wheat populations, likely due to the presence of higher gene flow. The STRUCTURE analysis detected three sub-groups ($\Delta K = 3$), with a greater degree of genetic admixture. Similar high genetic admixture and weak population clustering in wheat were reported by Deepender et al., (2019). In contrast, a more structure, i.e., 5-6 genetically distinct groups in accordance with their geographical area of sampling, was reported for Indian and Turkish wheat genotypes (Khan et al., 2015). This kind of sharp clustering might be due to low genetic intermixing and low gene flow.

4.2 Genetic variability, heritability and GxE interaction of bread wheat genotypes

4.2.1 Result

4.2.1.1 Genetic parametric analysis

4.2.1.1.1 Estimation of analysis of variance

In this study, a total of 12 quantitative traits were analyzed for superior germplasm selection. The analysis of variance (ANOVA) of the quantitative traits revealed highly significant ($p \leq 0.01$) variation for all traits studied. For replication, all the variables showed a highly significant difference ($p \leq 0.01$) except spike length and number of kernels per spike (Table 13, Table 21). Mean grain yield per plot, with the top-most mean yield recorded for accession G 147 (304.131 grams), while the lowest was G139 (188 grams). Estimates of phenotypic variance (δ^2p), genotypic variance (δ^2g), phenotypic coefficient of variation (PCV) and genotypic coefficients of variation (GCV) are given in Table 14. The phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) ranged from 1.98% (days to maturity) to 20.95% (spike weight) and 1% (days to maturity) to 11.26% (spike weight), respectively. Largely, the PCV values were higher than the GCV values for all the traits studied reflecting the influence of environment on the expression of all the traits. Deshmukh and Reddy (1986) classified PCV and GCV values as low (0 -10%), moderate (10-20%) and high (20% and above). Based on this delineation, characters which showed moderate phenotypic and genotypic coefficients of variation were number of kernels per spike, spike weight and grain yield per plot. This indicates that selection of genotypes with high potential would be effective based on these characters and their phenotypic expression. Leaf area and thousand kernel weights were found to be medium for PCV while low for GCV.

4.2.1.1.2 Heritability and genetic advance

An estimate of genetic advance is useful as a selection tool when considered jointly with heritability estimates (Azene, 2021). Moreover, estimates of genetic advance help in understanding the type of gene action involved in the expression of various polygenic characters. Likewise, the genotypic coefficients of variation along with heritability estimates provide reliable estimations of the amount of genetic advance to be expected through phenotypic selection. Heritability values are classified (Robinson et al., 1949) as

high (>60%), moderate (30-60%) and low (less than 30%). Accordingly, results of the present study indicated moderate heritability values in the number of kernels per spike (50%), plant height (50%), thousand kernel weight (41%), spike length (38%), and spike weight (30%). Moderate heritability values for these traits indicated that the variation observed was under genetic control and with considerable environmental influence. Similarly, Falconer and Mackay (1996) classified genetic advance as a percent of the mean as low (0-10%), moderate (10-20%) and high (20% and above). For grain yield per plot, genetic advance as a percentage of the mean was moderate (30.14%). Likewise, the genetic gain was moderate (13.96%) for the number of kernels per spike, followed by the weight of a thousand kernels (12.74%) and the spike (12.47%) (Table 14).

Table 14. Variance components, heritability, and genetic advances of the 12 agro-morphological traits of 178 wheat genotypes based on pooled data from three environments.

Traits	Range	SD	Mean	CV	σ^2_g	σ^2_p	σ^2_e	GCV	PCV	H^2	GA	GAM%
FD	3.63***	0.003**	71.05	8.6	2.25***	10.85***	15.8921***	2.11	4.64	0.21	1.41	1.98
HD	5.75***	3.08***	82.68	3.57	3.62***	12.34***	15.7361***	2.3	4.25	0.29	2.12	2.57
MD	0.82***	0.00***	143.3	1.71	2***	8.04***	15.0180***	1	1.98	0.25	1.45	1.01
LA	0.036*	0.00***	35.52	13.16	7.99***	29.85***	50.8335***	7.96	15.38	0.27	3.01	8.48
PH	3.47***	3.37***	87.72	4.29	14.23***	28.39***	33.59998***	4.3	6.07	0.5	5.5	6.27
SL	0.54 ^{ns}	7.32***	9.33	5.69	0.17***	0.45***	0.816983***	4.44	7.21	0.38	0.53	5.63
TKW	1.30***	5.84***	34.4	11.65	11.08***	27.15***	22.3991***	9.68	15.15	0.41	4.38	12.74
NSsS	3.38***	0.01**	17.87	6.22	0.28***	1.52***	3.013949***	2.97	6.89	0.19	0.47	2.63
NKS	0.7835 ^{ns}	2.71***	37.48	9.5	12.83***	25.51***	39.2153***	10.56	13.48	0.5	5.23	13.96
NKSs	0.56 ^{ns}	0.00**	3.1	10.44	0.03***	0.13***	3.099120***	5.5	11.8	0.22	0.16	5.29
SW	0.0004***	3.98***	2.39	17.67	0.07***	0.25***	0.153817***	11.26	20.95	0.30	0.3	12.47
GYPP	0.009**	3.20***	265.6	15.83	731.3***	2499***	2682.409***	10.18	18.82	0.29	30.14	11.35

SD = standard deviation, CV = coefficient of variation, HD = days to heading, FD = days to flowering, DM = days to maturity, TKW = thousand kernel weight, LA = leaf area, PH = plant height, SL = spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot, σ^2_g = Genotypic variance estimate, σ^2_p = phenotype variance estimate, σ^2_e = residual variance estimate, GCV = Genotypic coefficient of variance, PCV = Phenotypic coefficient of variance, GA = Genetic advance, $|H^2|$ =broad sense heritability, GAM = Genetic advance as percent mean, P-values: *** = very highly significant at $p < 0.001$, ** = highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

4.2.1.2 Clustering analysis

In clustering analysis, the number of clusters was determined using k-means clustering. The within sum of squares (wss) was drawn according to the number of clusters and location of a bend (knee) in the plot, in which the bend is generally considered an indicator of the appropriate number of clusters (Alboukadel, 2017). In addition to the wss method (Figure 14A) average silhouette method's pick indicates five numbers of clusters (Figure 14B).

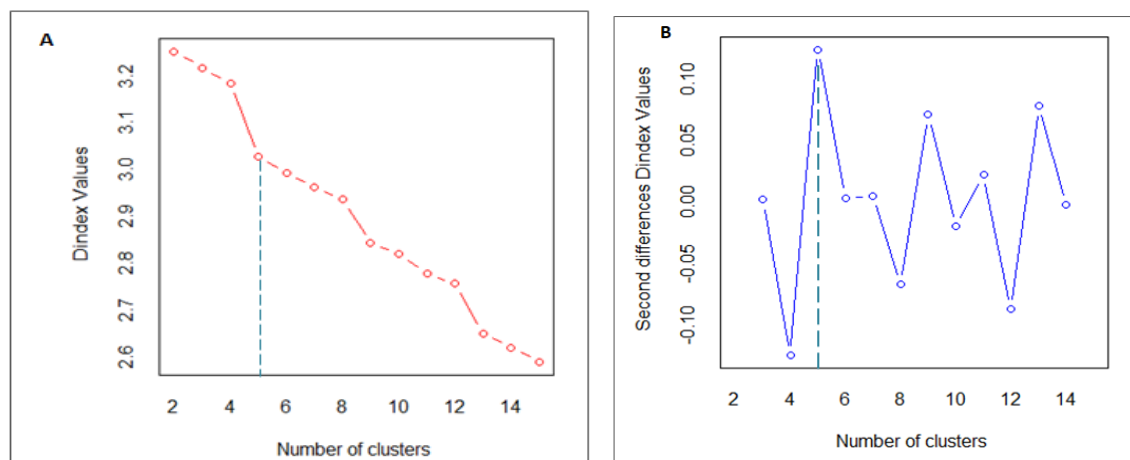


Figure 14. Number of clusters determined using wss (A), within sum of square method and (B), average silhouette method

Cluster analysis based on the unweighted pair group method with arithmetic averages (UPGMA) of the 12 agro-morphological traits revealed the presence of five distinct clusters. The dendrogram (Figure 15) was generated to examine the relationships among 180 bread wheat genotypes. As a result, range of various clusters showed the existence of large enough genetic divergence among the germplasm for the traits studied. Furthermore, the study illustrated the diversity of bread wheat genotypes among 167 recombinant inbred lines and 13 released varieties.

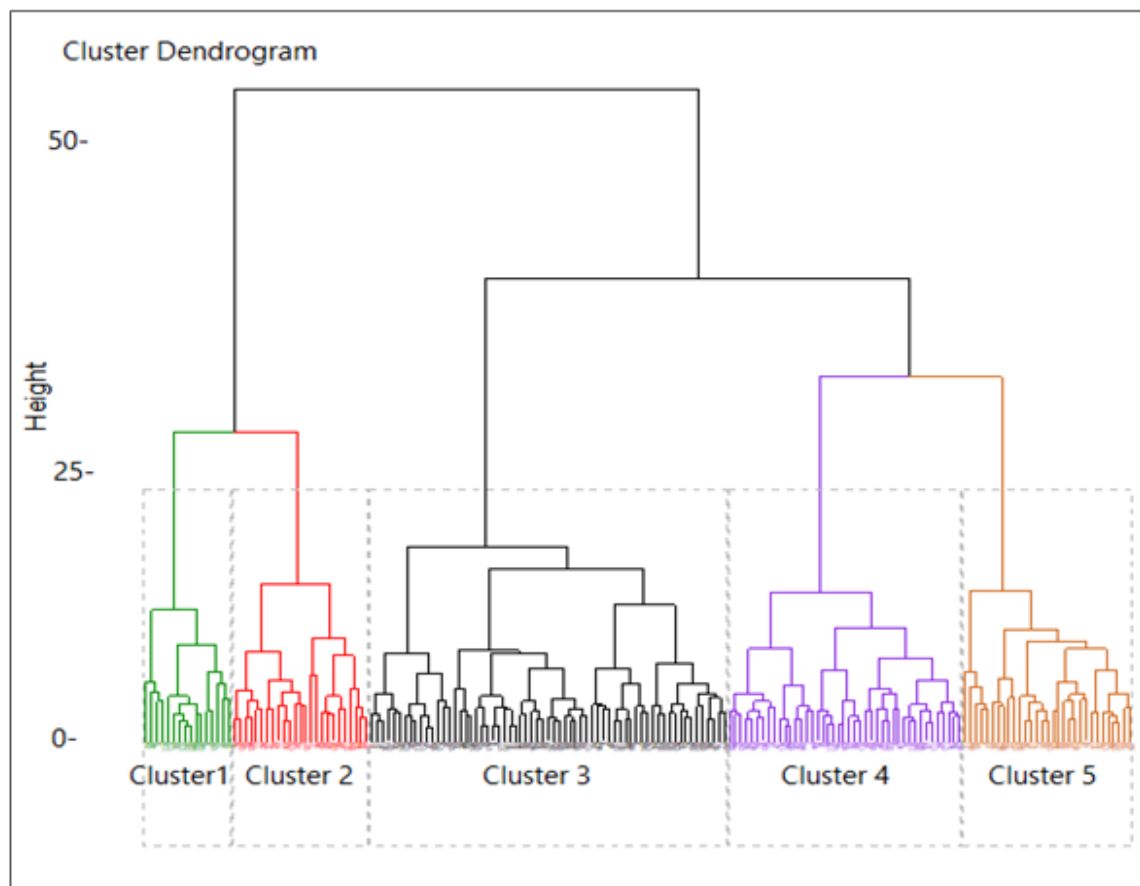


Figure 15. Cluster analysis revealed a dendrogram for 180 bread wheat genotypes based on UPGMA method of average clustering

Based on average method analysis, 180 genotypes were grouped into five clusters with a variable number of genotypes, suggesting considerable amount of genetic diversity in the genotypes (Figure 15). Among the clusters, cluster 3 was the largest, with 65 (36.11%) genotypes, indicating overall genetic similarity among them, followed by clusters 4 and 5 with 43 (23.89%) and 31 (17.22%) genotypes, respectively. Whereas cluster 1 with 16 (8.89%) and cluster 2 with 25 (13.89%) are clusters with fewer genotypes. More than average yield was recorded for cluster 3 (293 gram per plot) and cluster 5 (282 grams per plot). This implies that cluster 3 and 5 contain high yielding genotypes that produce more than 262 grams yield per plot with the required traits (Table 15).

Table 15. Relative proportion of average grand yield for five clusters revealed by cluster analysis of bread wheat genotypes

Cluster	Germplasm no	Genotypes	Average yield in gram	RPGY grams per plot
Cluster 1	16(8.89%)	24, 48, 5, 114, 173, 99, 172, 135, 149, 134, 148, 8, 128, 12, 30 and 4	244	-17.4
Cluster 2	25 (13.89%)	76, 139, 75, 126, 11, 26, 27, 29, 77, 63, 175, 20, 7, 127, 17, 36, 56, 65, 140, 49, 121, 109, 64, 43 and 87	223	-39.3
Cluster 3	65 (36.11%)	31, 41, 101, 137, 93, 145, 113, 32, 118, 112, 37, 108, 174, 18, 125, 33, 46, 54, 146, 129, 10, 176, 6, 177, 141, 81, 97, 82, 90, 162, 83, 89, 147, 102, 105, 68, 95, 152, 55, 117, 34, 164, 2, 45, 131, 151, 58, 150, 3, 144, 170, 94, 154, 155, 153, 178, 53, 74, 156, 132, 159, 96, 107, 71 and 100	293	+30.9
Cluster 4	43 (23.89%)	158, 79, 120, 60, 163, 70, 136, 13, 47, 116, 66, 143, 62, 165, 1, 69, 16, 15, 119, 142, 72, 103, 52, 86, 115, 39, 106, 40, 122, 123, 9, 61, 19, 110, 180, 160, 57, 111, 28, 171, 67, 44 and 161	248	-14
Cluster 5	31 (17.22%)	21, 166, 59, 4, 23, 80, 167, 169, 22, 124, 168, 38, 51, 73, 35, 138, 84, 85, 98, 25, 104, 14, 78, 91, 92, 179, 88, 130, 133, 50 and 157	282	+19.7

Note: grand average yield: 262 grams per plot; RPGY: relative proportion of grand average yield; '(+)' : yield higher; '(-)' : yield lower.

Intra-clustering and inter-cluster distances were analyzed to study the degree of divergence between clusters. According to inter-cluster distance values between the five clusters, the highest distance was exhibited between clusters 1 and 2 (130.45), followed by clusters 2 and 4 (97.13) and cluster 4 and 5 (71.3944), indicating wider genetic divergence among the clusters (Table 16). Thus, crossing of genotypes between members of 1 and 5 may produce high amount of heterotic expression.

Table 16. Inter cluster values among five clusters using 12 agro-morphological traits.

	Cluster1	Cluster2	Cluster3	Cluster4	Cluster5
Cluster1	****				
Cluster2	130.45	****			
Cluster3	68.643	61.8431	****		
Cluster4	33.396	97.1303	35.2942	****	
Cluster5	104.72	25.789	36.1245	71.3944	****

Intra-cluster distance values of the five clusters with the number of observations, within cluster sum squares, average distance from the centroid and maximum distance from

centroid are presented in Table 17. The lowest average distance from centroid were noted in cluster 5 (10.526) followed by cluster 1 (10.919) indicating the presence of divergence. The highest average distance from centroid was exhibited in cluster 3 (13.526) followed by cluster 2 (12.9003) and cluster 4 (12.1006). This indicates that crossing bread wheat germplasm of cluster III can produce a broad spectrum of variability.

Table 17. Intra clustering of five clusters of 180 bread wheat genotypes using 12 quantitative traits

Clusters	Number of observations	Within cluster sum squares	Average distance from centroid	Maximum distance from centroid
Cluster1	16	2222.3	10.919	19.6347
Cluster2	25	5728.4	12.9003	26.9575
Cluster3	65	14344.7	13.526	24.633
Cluster4	43	5393.1	12.1006	19.8635
Cluster5	31	3929.6	10.526	19.8146

4.2.1.3 Principal component analysis

The PCA of the 180 bread wheat genotypes based on the 12 agronomic traits resulted in 12 principal components. The first, five principal components (PC) had accounted for 76.25% of the cumulative variation (Table 18). The 1st PC gained and recorded the topmost proportion of the variance in the set of all PCs and rest was gradually smaller amounts of variation. However, the percent of variation for PC1 and PC2 was 31.59% and 18.98%, respectively. The graphical illustration of 180 genotypes exposed by principal component analysis (PCA) was shown in Figure 16. The traits contributing to PC1 and PC2 are showed topmost variability with a high coefficient of variation. PC1 allowed loading of yield related traits like total spike weight (19), number of kernels per spike (14.92), thousand kernel weight (13.25), grain yield (12.97) and number of kernels per spikelets (11.82) indicating the significance for the respective principal components simultaneously. PC2 allowed loading of phenological traits; day to heading (31.53), day to flowering (24.11) and day to maturity (17.13). Furthermore, PC3 allowed loading of vegetative traits; spike length (49.86), plant height (10.66) and yield related trait number of kernel per spikelets (8.5), for PC 4 number of spikelets per spike (42.31), plant height

(16.64cm) and days to flowering (10.68) indicates significance for respective principal components simultaneously.

The relationship between eigenvalues and principal component and their proportion of variation are presented in Table 18.. Figure 16 demonstrates most of the accessions were dispersed at low distances, whereas a few were dispersed at high distances, as reflected by an eigenvector. The outermost genotypes from the centroid were G4, G7, G8, G12, G17, G21, G22, G23, G26, G27, G34, G36, G49, G50, G63, G77, G109, G129, G124, G127, G128, G154, G166, and G175 whereas other genotypes were near to the centroid.

Table 18. Coordinates and statistics of the principal components (PCs) analysis of 12 traits

Traits	PC1	PC2	PC3	PC4
FD	4.74	24.11	2.81	10.68
HD	2.50	31.53	0.71	8.44
MD	0.14	17.13	4.33	0.21
GY	12.97	1.63	1.75	5.65
TKW	13.25	2.58	0.02	5.70
LA	8.45	1.42	9.72	4.25
PH	7.52	0.37	10.66	16.64
SL	2.28	3.15	49.86	3.51
NSsS	2.42	8.65	0.16	42.31
NKS	14.92	4.56	4.95	1.57
NKSs	11.81	3.86	8.50	0.83
SW	19.00	1.01	6.53	0.21
eigenvalue	3.79	2.28	1.15	1.07
variance%	31.59	18.98	9.57	8.90
cumulative variance%	31.59	50.58	60.15	69.05

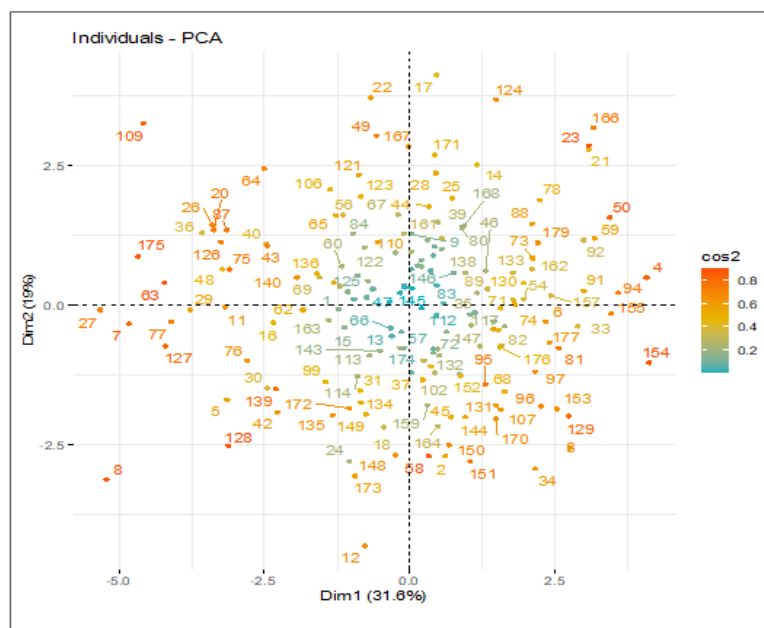


Figure 16. Principal components plot of 180 bread wheat genotypes based on 12 traits.

4.2.1.4 Analysis of correlation matrix

Phenotypic and genotypic correlation evaluations between all pairs of the 12 agronomic traits considered for the 180 bread wheat genotypes studied are presented in Table 19. The analyses indicated that highly significant positive phenotypic association between days to heading and days to flowering (0.97), followed by number of kernels per spike and number of kernels per spikelets (0.93) and number of kernels per spike and spike weight (0.87). Strong negative phenotypic correlation was recorded between days to flowering and thousand kernel weight (-0.52), followed by days to flowering and plant height (-0.50), and days to heading and thousand kernel weight (-0.42). Likewise, a strong positive genotypic association was observed between days to heading and days to flowering (0.97), followed by the number of kernels per spike and number of kernels per spikelets (0.93) and number of kernels per spike and spike weight (0.88) were noted. Also, a strong negative genotypic correlation was detailed between thousand kernel weight and days to flowering (-0.52), followed by plant height with days to flowering (-0.49), and thousand kernel weight and days to heading (-0.42).

Table 19. Phenotypic correlation (above diagonal) and genotypic (below diagonal) correlation of 12 agronomic traits Of bread wheat genotypes

Traits	HD	FD	MD	TKW	LA	PH	SL	NSsS	NKS	NKSs	SW	GYPP
HD	***	0.97***	0.47***	-0.42***	0.05 ^{ns}	-0.24***	0.10 ^{ns}	0.56***	0.10 ^{ns}	0.03 ^{ns}	-0.11 ^{ns}	-0.24***
FD	0.97***	***	0.44***	-0.52***	0.11 ^{ns}	-0.50***	-0.10 ^{ns}	0.70***	0.10 ^{ns}	-0.13 ^{ns}	-0.14 ^{ns}	-0.32***
MD	0.47***	0.44***	***	0.13 ^{ns}	0.46***	-0.13 ^{ns}	0.40***	0.73***	0.11 ^{ns}	0.18***	0.42***	-0.07 ^{ns}
TKW	-0.42***	-0.52***	0.13 ^{ns}	***	0.56***	0.31***	0.17***	0.20***	0.47***	0.29***	0.73***	0.80***
LA	0.05 ^{ns}	0.11 ^{ns}	0.46***	0.56***	***	0.44***	0.51***	0.28***	0.51***	0.81***	0.47***	0.27***
PH	-0.24***	-0.49***	-0.13 ^{ns}	0.31***	0.44***	***	0.29***	-0.03 ^{ns}	0.34***	0.31***	0.22***	0.49***
SL	0.10 ^{ns}	-0.10 ^{ns}	0.40***	0.17**	0.50***	0.29***	***	0.42***	0.24***	0.31***	0.20***	0.04 ^{ns}
NSsS	0.56***	0.70***	0.73***	0.20***	0.28***	-0.03 ^{ns}	0.42***	***	0.60***	0.78***	0.50***	0.00 ^{ns}
NKS	0.10 ^{ns}	0.10 ^{ns}	0.11 ^{ns}	0.47***	0.51***	0.34***	0.24***	0.60***	***	0.93***	0.87***	0.49***
NKSs	0.03 ^{ns}	-0.13 ^{ns}	0.175*	0.29***	0.80***	0.31***	0.32***	0.78***	0.93***	***	0.84***	0.50***
SW	-0.11 ^{ns}	-0.14 ^{ns}	0.42***	0.70***	0.47***	0.23***	0.20***	0.50***	0.88***	0.84***	***	0.52***
GYPP	-0.24***	-0.32***	-0.07 ^{ns}	0.80***	0.23***	0.49***	0.03 ^{ns}	0.00 ^{ns}	0.49***	0.50***	0.51***	***

Trait abbreviations are: HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot. P-values: *** = very highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

A correlations dendrogram of 12 agronomic traits and a graph of 180 bread wheat genotypes result in three groups; the first group includes two phenological traits: days to flowering and days to heading. Also, the second group combines yield-related and phenological traits: days to maturity, spike length and number of spikelets per spike. Similarly, the third group also includes all vegetative traits and many yields related traits: number of kernels per spikelet, number of kernels per spike, leaf area, spike weight, thousand kernel weight, grain yield per plot and plant height. The genetic correlations between the 12 traits also revealed that heading date was negatively correlated to other traits, as shown in Figure 17A. In the graph, 84.22% of the total variations were explained by two principal components, accounting for 65.15% and 19.09% for PC1 and PC2 respectively (Figure 17B).

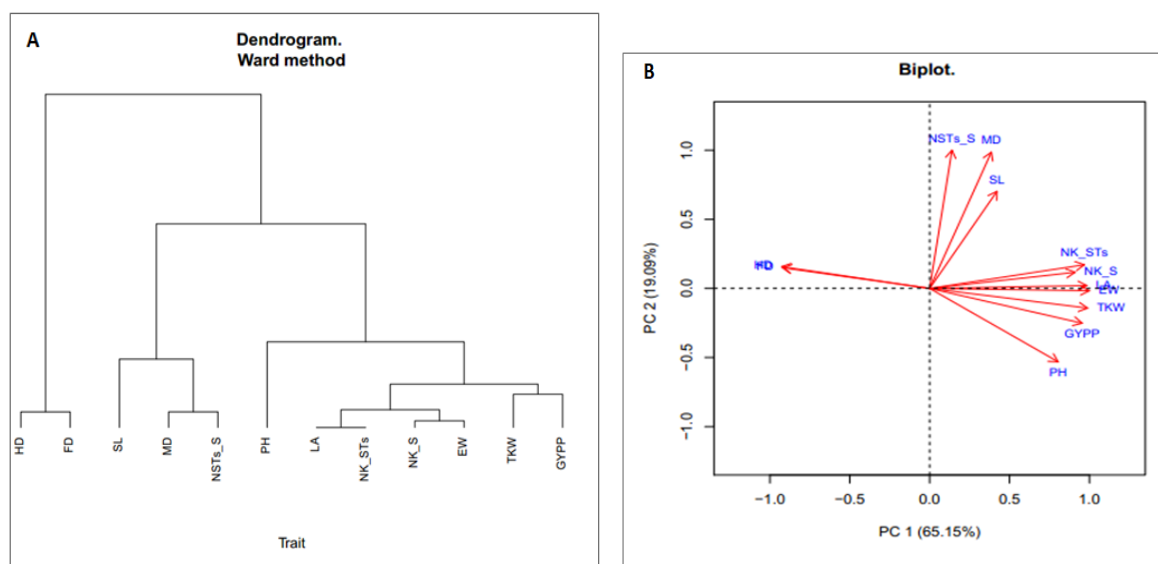


Figure 17. A) Agronomic traits dendrogram B) Graph of genotypic correlations combined for all environments of ten traits. Trait abbreviations are: HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot.

4.2.1.5 Path coefficient analysis

Since path coefficient analysis measures the direct and indirect contributions of independent variables to dependent variables, it helps the breeder consider the reason for the association between variables. In this study, the 12 agronomic traits were examined for their direct and indirect effects on grain yield per plot using path

coefficient analysis at the phenotypic and genotypic levels using the dependent (response) variable grain yield per plot (GYPP) and the remaining 10 independent (predictor) variables. At the phenotypic level, the highest positive direct effects were exhibited by thousand kernel weight (0.12), followed by number of kernels per spike (0.10) and days to maturity (0.08). Besides, the number of kernels per spike and days to maturity can be negatively affected by number of spikelets per spike (-0.03) and days to heading (-0.10) respectively. On the other hand, the maximum negative direct effect was exhibited by days to heading (-0.11), followed by number of spikelets per spike (-0.09) and the number of kernels per spikelet (-0.04). Consistently, highest positive indirect effect was revealed by spike weight (0.07), via thousand kernels weight followed by spike weight via number of kernels per spike (0.06) and days to heading via days to flowering (0.06) and number of kernel per spikelet (0.05) through number of kernel per spike. Furthermore, the highest negative indirect effect was revealed by days to flowering (-0.10) via days to heading followed by days to maturity (-0.05) via days to heading and days to flowering (-0.04) through thousand kernel weight (Table 20).

Table 20. Path coefficients analysis of direct (bold main diagonal) and indirect (off-diagonal) of yield contributing traits on bread wheat yield at phenotypic level

Traits	FD	HD	MD	TKW	LA	PH	SL	NSsS	NKS	NKSs	SW
FD	0.07	-0.10	0.03	-0.04	0.00	-0.01	0.00	0.00	-0.01	0.00	0.01
HD	0.06	-0.11	0.03	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	-0.01
MD	0.03	-0.05	0.08	0.00	0.00	0.00	0.01	-0.01	0.01	0.00	0.00
TKW	-0.02	0.03	0.00	0.12	0.00	0.02	0.00	0.00	0.03	0.00	0.02
LA	-0.01	0.01	0.01	0.03	0.00	0.02	0.01	-0.01	0.03	0.00	0.01
PH	-0.01	0.01	0.00	0.03	0.00	0.06	0.01	0.00	0.03	0.00	0.01
SL	0.00	0.00	0.01	0.01	0.00	0.01	0.04	-0.02	0.02	0.00	0.01
NSsS	0.00	0.00	0.01	0.00	0.00	0.00	0.01	-0.09	0.03	0.00	0.01
NKS	0.00	0.00	0.01	0.04	0.00	0.03	0.01	-0.03	0.10	0.02	0.03
NKSs	0.00	0.00	0.01	0.03	0.00	0.01	0.00	-0.01	0.05	0.04	0.02
SW	-0.02	0.03	0.01	0.08	0.00	0.03	0.01	-0.02	0.06	0.02	0.04

Trait abbreviations are: HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GY=grain yield per plot.

Direct and indirect effects of traits on grain yield analyzed at genotypic level presented in Table 21 revealed that the highest positive direct effects on yield were exhibited by days to heading (4.49), followed by number of kernels per spikelets (2.87) and thousand

kernel weight (2.72). On the other hand, the maximum negative direct effect was exhibited by days to flowering (-4.57), followed by spike weight (-3.74) and spike length (-1.95). Moreover, the highest positive indirect effect was revealed by days to flowering (4.37) via days to heading followed by number of kernels per spike (2.66) via number of kernels per spikelet and number of speculates per spike (2.49) through days to heading. Additionally, the highest negative indirect effect was revealed by days to heading (-4.57) via days to flowering, followed by number of kernels per spike (-3.27), via spike weight and number of kernels per spikelet (-3.16) through spike weight.

Table 21. Path coefficients analysis of direct (bold main diagonal) and indirect (off-diagonal) of yield contributing traits on bread wheat yield at genotypic level

	FD	HD	MD	TKW	LA	PH	SL	NSsS	NKS	NKSs	SW
FD	-4.57	4.37	0.20	-1.41	0.00	0.38	0.19	0.07	-0.02	-0.37	0.52
HD	-4.45	4.49	0.21	-1.13	0.00	0.18	-0.20	0.06	-0.02	0.09	0.43
MD	-2.00	2.12	0.44	0.35	-0.02	0.10	-0.77	0.08	-0.02	0.50	-1.56
TKW	2.36	- 1.86	0.07	2.72	-0.03	-0.23	-0.33	0.02	-0.10	0.84	-2.74
LA	-0.50	0.24	0.20	1.52	-0.04	-0.34	-0.98	0.03	-0.10	2.32	-1.77
PH	2.24	- 1.09	-0.06	0.84	-0.02	-0.76	-0.57	0.00	-0.07	0.88	-0.81
SL	0.44	0.47	0.18	0.47	-0.02	-0.22	-1.95	0.04	-0.05	0.91	-0.74
NSsS	-3.21	2.49	0.32	0.55	-0.01	0.02	-0.81	0.11	-0.12	2.25	-1.85
NKS	-0.46	0.44	0.05	1.27	-0.02	-0.26	-0.47	0.06	-0.20	2.66	-3.27
NKSs	0.59	0.15	0.08	0.80	-0.03	-0.23	-0.61	0.08	-0.19	2.87	-3.16
SW	0.64	- 0.50	0.18	2.00	-0.02	-0.17	-0.33	0.05	-0.18	2.43	-3.74

Trait abbreviations are: HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot.

4.2.1.6 Genotype - environment interaction

4.2.1.6.1 ANOVA analysis

The mean squares of the 12 characters from the analysis of variance (ANOVA) presented in Table 22 were highly significant ($P < 0.01$) for all traits. This indicates that significant variability among the germplasm studied and that would respond positively to selection.

Table 22. Combined ANOVA for grain yield and its components and description of phenotypic data for agronomic traits (MS and CV analysis of all variables over three environments)

Source	L	LxR	LxRxB	G	Gx L	LSD /SE	CV%
DF	2	3	58	179	358		
FD	250420.35***	303.89***	54.80***	46.78***	18.93***	3.98	4.81
HD	220275.35***	309.76***	59.41***	37.66***	18.85***	3.92	5.52
MD	328207.10***	134.06***	58.38***	26.80***	19.84***	4.02	2.8
GYPP	783870.***	13421**	6128***	9051***	2662***	51.6	19.45
TKW	102738.30***	1302.93***	42.79***	110.37***	17.29***	4.42	12.84
M LA	37748.09***	768.67***	87.98***	110.24***	74.15	6.85	19.28
S PH	16422.50***	1153.33***	152.89***	108.31***	41.38	5.70	6.5
SL	162.14***	3.4357**	1.27**	1.86***	0.83	0.90	9.6
NSsS	70.69***	101.84***	7.01***	4.78***	3.02	1.73	9.68
NKS	207858.03***	146.67**	64.39**	112.62***	55.81	6.30	16.82
NKSs	59.5749***	1.6265***	0.96***	0.43***	0.40	0.54	17.47
SW	22.73***	1.09***	0.30***	0.38***	0.17	0.38	17.64

Trait abbreviations are: L=location, R=replication, B=block, G=genotype, SLD=least significant difference, CV=coefficient of variation, DF=degree of freedom, MS=mean square error. HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot. P-values: *** = very highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

4.2.1.6.2 AMMI analysis

As provided by the AMMI analysis of variance for grain yield per plot in 180 bread wheat plots there were highly significant genotypic, environmental and genotype-environmental interaction effects ($p < 0.001$). The combined analysis of variance and AMMI analysis shown in Table 23 indicated highly significant differences for environment and genotype. In this study, the wheat genotype grain yields were significantly affected by the environment, accounted for 55.22% of the total (G + E + GE) variation, whereas genotype and genotype-environment interaction accounted for 27.46% and 17.44%, correspondingly. Out of the interaction sum of squares, 48.14% was explained by IPCA1 and IPCA2. Therefore, the AMMI model is somewhat informative to explore the adaptation of the germplasm.

Table 23. Combined AMMI analyses of variance and contributions of the first two PCAs to the grain yield of 180 bread wheat genotypes in 3 environments

Source	Df	SS	MS	G+E+GE MS (%)	GE SS (%)
G	179	4.19	3.67 **	27.46	
E	2	2.83	7.41 *	55.22	
GxE	358	1.31	2.34 ***	17.44	
IPCA1	180	2.31	7.29 ***		47.93
IPCA2	178	0.01	0.00 ***		0.21
Residuals	1	2.50	2.50 **		

DF = degree of freedom; SS = sum of squares; MS = mean square; IPCA = interaction principal component axis; P-values*** = very highly significant at $p < 0.001$, ** = highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

4.2.1.6.2.1 AMMI biplot analysis

AMMI biplot constructed for wheat grain yield per plant (GYPP) the horizontal axis describes the main effect and the vertical axis describes variation of the multiplicative effects in genotype environment-interaction (GEI) (PCA1) with a score of 76.28% (Figure 19). Numerous genotypes showed a biplot with the lowest IPCA1 scores closest to zero, such as G48, G3, G150, G178, G100, G95, G50, G83, G138 and G33, which can be recommended as stable genotypes with a yield greater than the mean grain yield. The AMMI1 biplot for grain yield also clearly indicated that the three environments differed in both main and interaction effects. Accordingly, Meraro environment was favorable for a mean grain yield below the mean whereas, the Holeta and Kulumsa environments were favorable for most of the genotypes with an above average mean grain yield. Pattern analysis on the first interaction principal components axes (IPCA1) and mean of GYPP divided the genotypes and environments into two groups of medium and low grain yield (GYPP), were separated and located in different groups. Holeta and Kulumsa were in the first group with medium IPCA1 scores and good grain yield. Whereas Meraro were out-grouped containing germplasm with below-average grain yields (Figure 18) (Table 24).

Table 24. List of Top 33 high yielder bread wheat genotypes used for GGE and AMMI analysis

Location	G3	G9	G13	G30	G33	G46	G47	G50	G53	G54	G55
MER	227.66	246.83	230.68	211.83	240.83	231.26	220.24	232.42	231.84	208.64	207.19
KUL	387.70	346.53	359.50	384.70	392.25	381.25	358.50	356.25	387.25	377.50	395.00
HOL	363.80	341.35	375.00	321.80	353.50	359.50	381.00	359.50	413.50	337.00	332.00
AVE	326.39	311.57	321.73	306.11	328.86	324.00	319.91	316.06	344.20	307.71	311.40
Location	G58	G68	G82	G92	G94	G95	G96	G97	G100	G102	G138

MER	205.74	241.12	239.96	233.58	218.50	215.02	197.91	215.02	208.64	205.16	215.89
KUL	396.83	383.50	365.50	358.50	344.00	372.05	362.68	358.00	364.25	385.00	384.50
HOL	306.55	411.00	369.00	381.00	368.00	346.70	300.45	324.00	361.50	312.00	345.00
AVE	303.04	345.21	324.82	324.36	310.17	311.26	287.01	299.01	311.46	300.72	315.13
Location	G150	G153	G157	G158	G159	G162	G168	G170	G174	G177	G178
MER	204.29	242.86	210.09	207.77	205.45	234.74	243.15	230.10	245.76	206.03	216.18
KUL	385.25	361.13	379.53	387.63	355.75	369.25	381.13	340.50	379.35	386.00	363.00
HOL	365.50	367.75	338.35	323.75	312.50	371.50	417.75	379.00	379.90	306.00	344.00
AVE	318.35	323.91	309.32	306.38	291.23	325.16	347.34	316.53	335.00	299.34	307.73

Trait abbreviations and locations are: G=genotype, HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot, MER=Meraro, KUL=Kulumsa, HOL=Holeta.

4.2.1.6.2.2 AMMI2 biplot analysis

AMMI2 biplot analysis (PCA1 vs. PCA2 biplot) describes the genotype by environment interaction (GEI) in which genotypes and environments farther from the center of the biplot are considered to have a large genotype by environment interaction and show specific adaptation, whereas, genotypes near the origin are considered to have better stability. The AMMI2 biplot accounted for a total sum of squares for 100% for GEI. The result of this biplot G98, G49, G115, G119, G86, G65, G173, G29, G108, G120, G10, G19, G133, G66, G149, G89, G108, G133, G4, G17 and G148 scattered close to the origin of biplot are stable. Among them, the genotypes G3, G48, G100, G150, and G95 display productivity above the grand mean (266.98 gm per plot), indicating their productive and stable performance (Figure 18). This implies that these genotypes have better adaptability and stability. On the other hand, genotypes G55 and G58 with high mean performance can-not be stable. Besides, genotypes G55 and G58 showed a specific adaptability to Kulumsa, genotypes G53, G168 and G68 to Holeta and genotypes G160 and G106 to Meraro (Figure 18).

Since the nature of the interaction effect has been explained with the angle between vectors of germplasm and environment, result, the interaction effect for acute angles is positive. Interaction effects for right angles are negligible interaction and negative for obtuse angles. On this basis, genotypes listed in their environments showed an acute angle and acceptable mean grain yield, which indicated specific and wide adaptation depending on the closeness to the origin. For example, germplasm G20 and G8 have an acute angle interaction with each other and with Kulumsa and they are far from the origin. Besides, they have an obtuse angle of interaction with the genotypes that existed

under Holeta meaning that they have negative GEI with Holeta environments and with genotypes that existed (Figure 18).

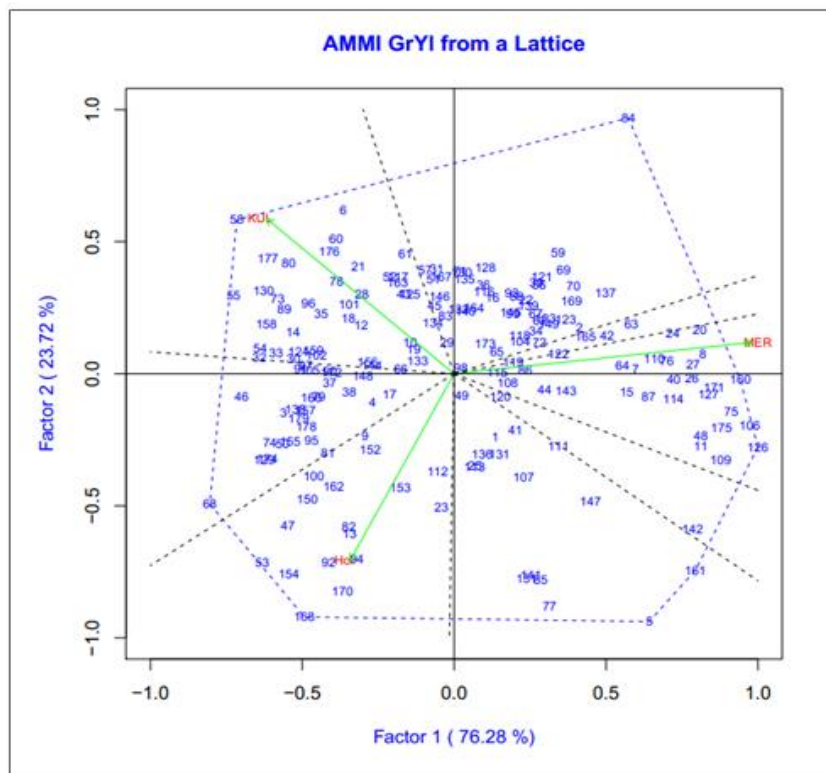


Figure 18.Biplot of the first two GEI principal component axes (PCA1 vs PCA2) for grain yield trait of the 180 bread wheat genotypes grown in three environments

4.2.1.6.2.3 GGE analysis

Only Axis 1 (75.99%) and Axis 2 (20.68%) of the principal components suited by the GGE Biplot analysis information relation retained patterns in the data. This shows that the first two principal components were adequate for visually representing the data (Figure 19). Based on grain yield mean the top 33 genotypes were selected. As a result from those selected genotypes the stable genotypes were G162, G82, G100, G95 and G46. Moreover, genotypes; G178, G157, G54, G157, G50, G13, G174, G3 and G138 were also relatively stable, whereas, genotypes G97, G30, G158, G55, G8, G168 and G53 were unstable and had large contribution to the genotype-by-environment interaction . Based on the AXIS scores Holeta and Kulumsa environments were far from the average environment coordination (AEC) and highly contributed to the genotype and environment interaction. Meraro location is near to the AEC (Figure 19) .

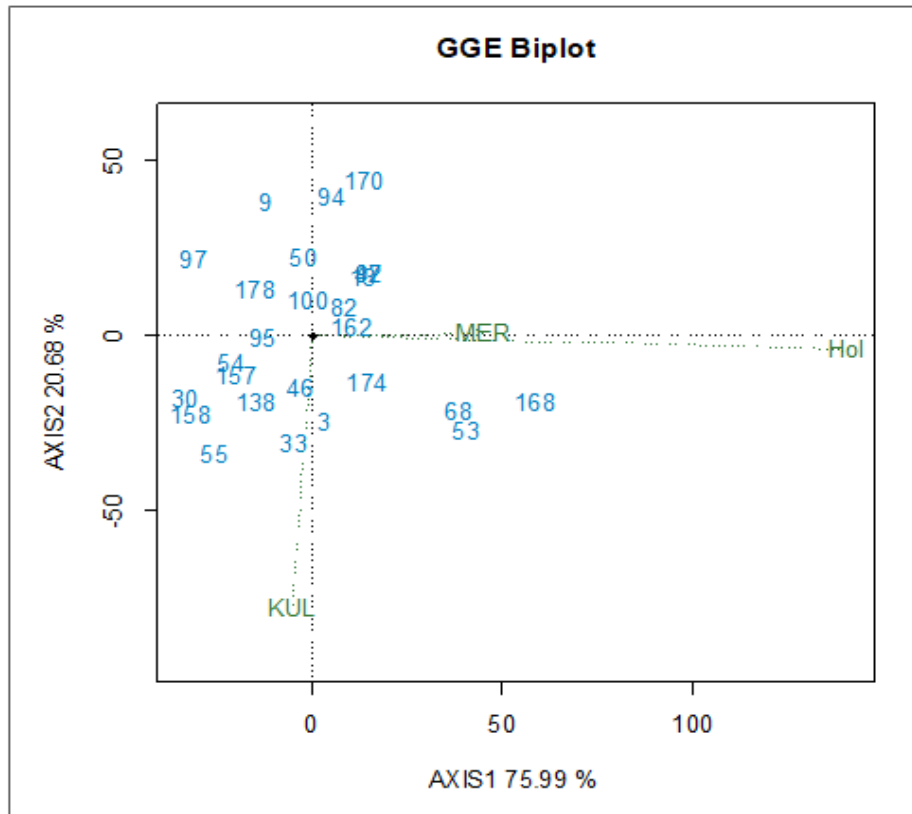


Figure 19. GGE biplot for mean grain yield per plot

Nominal yield and environment IPCA1 is used for possible mega-environments identification as well as visualizing the “which-won-where” pattern (VSN, 2015; Singh et al., 2017). In this graphic, each germplasm is depicted by a straight line, indication which germplasm in a given environment has the highest nominal yield in that environment. The line crossings between the winners confirm the presence of genotype-environment interactions (Figure 20).

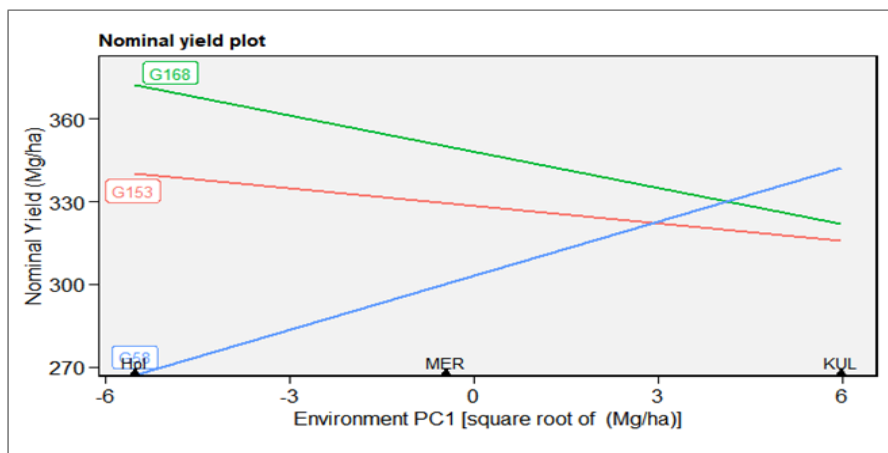


Figure 20. Nominal grain yield bread wheat genotypes according to the AMMI1 model, principal component (PC1) scores for the three environments, green = Holeta, blue=Kulumsa and red = Meraro)

Moreover, as displayed in Figure 21 ideal germplasm, represented by the small circle with an arrow pointing to it, is defined as having the highest yield and stable in all environments. As shown in Figure 21 ranking of the selected bread wheat genotypes based on their distance from the ideal germplasm, based on the graphical interpretation, genotypes G68 and G53, followed by G168, were considered yielder genotypes near the mean. Other genotypes lying on the right side of the line with double arrows had yield performance greater than the mean and the genotypes on the left side had yields lower than the mean (Figure 21).

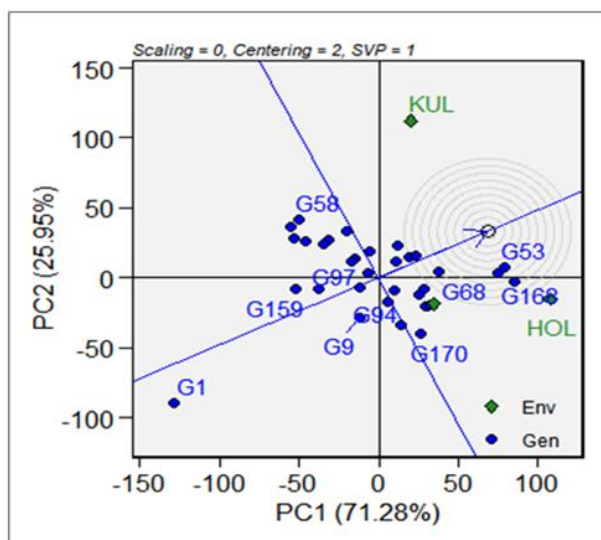


Figure 21. GGE biplot showing ranking of 33 genotypes for mean yield based on the “average environment coordinate” (AEC).

4.2.1.6.2.4 Ranking environments

As displayed in Figure 22, the “ideal” environment was used as the center of concentric lines that serve as a ruler to measure the distance between an environment and the ideal environment. Since Holeta is the closest to the ideal environment, it is the most preferable of all environments following by Meraro (Figure 22).

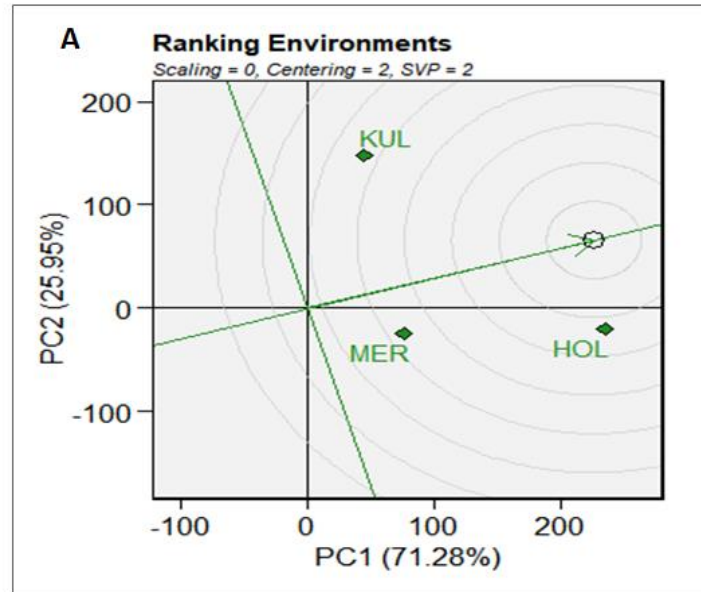


Figure 22. Discrimination and representativeness view of the GGE biplot to rank test environments relative to an ideal test environment (represented by center of concentric circles).

4.2. 2 Discussion

4.2.1.1 Estimation of analysis of variance

The findings of this work displayed the presence of significant variation among bread wheat genotypes estimated for 12 quantitative traits. Moreover, descriptive statistics analysis (averages, range and coefficient of variation) confirmed the existence of genetic diversity in the bread wheat germplasm. The analysis result of the mean squares of the traits in the present study revealed high significant difference ($p \leq 0.01$) among 180 bread wheat genotypes. Similarly other previous reports showed the existence of considerable diversity in some phonological, vegetative and yield and related traits (Berhanu et al., 2022; Obsa et al., 2016; Gerema et al., 2020; Destaw et al., 2020; Dabi et al., 2019; Hassani et al., 2022). Besides, (Hassani et al., 2022) measured highly significant genetic variation for grain yield and yield related traits in bread wheat lines. Highly significant difference ($p \leq 0.01$) in days to heading, days to maturity, plant height, and thousand-kernel weight were reported Endashaw et al., (2021). The significant differences among bread wheat genotypes under investigation indicate the presence of genetic variability in the material used and provide opportunity for yield improvement. Substantial variances were testified for bread wheat agronomic traits such as days to heading, days to maturity, plant height, spike length, number of spikelets per spike, thousand grain weights and grain yield per plot by Singh and Kumar, (2017) and Hassani et al., (2022). Likewise, Kumar et al. (2009) and Monpara (2011) reported

significant variability among 30 bread wheat genotypes for eight agronomic traits and among 21 bread wheat genotypes for 11 traits, respectively. This implies that there is a wide range of genetic diversity within bread wheat genotypes, which could be valuable for breeding programs aimed at improving agronomic traits. Moreover, Kalim et al., (2012) stated that grain yield per spike, thousand-kernel weight and grain yield per plant presented significant differences between 41 bread wheat genotypes. On the other hand Ali and Shakor, (2012) reported moderate PCV and GCV for grain yield per plot in 20 bread wheat genotypes. In addition, (Degewione and Alamerew, 2013) testified to moderate PCV and GCV for thousand grain weight, plant height and days to heading in 26 bread wheat genotypes. In contrast, the large differences in PCV and GCV show the large influence of the environment on the phenotypic expression of the other traits (Dragov et al., 2022). This suggests that genetic variability plays a significant role in determining the performance of different bread wheat genotypes under varying environmental conditions.

4.2.1.2 Heritability and genetic advance

Heritability is an important tool for the inheritance of a character and high heritability values show the least influence of environment. Furthermore, heritability contains the effects of both additive and non-additive genes. However, heritability alone is not adequate for selection processes. Heritability, along with the genetic advance as a percentage of mean (genetic gain), is crucial for effective selection. In this study, moderate heritability and genetic advance for the number of kernels per spike and plant height were observed. Moderate heritability associated with moderate genetic advance was observed for the number of kernels per spike, in accordance with previous reports by Sonal and Shukla (2022). Other studies noted high heritability estimates for the thousand kernel weights and plant height (Salem et al., 2008; Birhanu, 2016; Khan 2010; Birtucan et al., 2023). The variation observed in the current study and those studies was due to differences in environmental influence. Likewise, the expected genetic advance expressed as a percentage of mean of the bread wheat genotypes was moderate for grain yield per plot, plant height, and number of kernels per spike, thousand kernel weight, spike length, and spike weight. Similarly, Degewione and Alamerew (2013) recorded genetic progress as moderate for plant height. Likewise,

moderate to high genetic advances were reported for plant height and thousand kernel weights, in agreement with the present results (Kalim, 2012; Dagnaw et al., 2022).

4.2.1.3 Cluster and principal component analysis

Based on hierarchical clustering analysis, 180 genotypes were grouped into five distinct clusters, which were further divided into six sub-groups. This implies the existence of considerable variation among genotypes. Similar results were reported by Dotlail et al., (2000), in which the diversity might have resulted from genetic drift under diverse environmental conditions. The highest intercluster distance was perceived between clusters 1 and 2. Accordingly, genotypes from cluster 1 and cluster 2 can be used as parents in yield improvement breeding programs.

Principal component analysis is useful for identifying diverse genotypes. Wheat genotypes were placed in different groups according to their genetic variability. In the present study, the percent of variation for PC1, PC2, and PC3 was 31.59%, 18.98%, and 9.57%, respectively, with a cumulative variance of 60.14% out of the total phenotypic variance. Similar results were recorded by Mohammed (2014), who studied genetic diversity in 100 wheat genotypes and found that the variance of three PCs was 31.59%, 18.98%, and 9.57%, respectively, with a cumulative variance of 60.15 out of the total phenotypic variance. Furthermore, the principal component analysis result showed that the first two PCs have an eigenvalue greater than the other two, suggesting that yield-related traits such as spike weight, number of kernels per spike, thousand kernel weight, number of kernels per spikelet, and phenological traits such as day to heading, day to flowering, and day to maturity are valuable traits that significantly contribute to the total variation of the germplasm.

4.2.1.4 Correlation and path coefficient analysis

The phenotypic correlation indicated a highly significant positive association between days to heading and days to flowering (0.97) followed by number of kernels per spike and number of kernels per spikelets (0.93). Similar results were also reported by other researchers (Endashaw et al., 2021; Rangare et al., 2010; Baranwal et al., 2012). Likewise, genotypic correlation offers a measure of the genetic relationship between traits that could be used as a selection criterion in breeding programs. On the other

hand, the relationship between days to flowering and thousand kernel weight and plant height, followed by days to heading and thousand kernel weight, was negatively correlated. These outcomes suggested that selection of early heading and early flowering could improve a genotype's performance by thousand kernel weights. Similar results were reported by Fellahi et al. (2013). Moreover, correlations showed a slightly higher genotypic coefficient than phenotypic correlations in favour of a selection strategy for breeding programs since phenotypic correlations have genetic and environmental interactions but only associations of a genetic nature are inheritable (Fioreze and Rodrigues, 2012).

Furthermore, path coefficient analysis measures revealed that thousand kernel weight, number of kernels per spike, and days to maturity exerted the highest positive effect on grain yield, in agreement with results reported by Ajeet et al. (2022). Days to flowering also exerted the highest positive indirect effect via days to heading, which was also similar to reports by Mesele et al. (2016) and Gerema et al. (2020). Traits having a direct positive effect on grain yield could be directly selected for yield improvement programs; whereas traits with indirect effects could be considered as they have an association with those characters in another way.

4.2.1.5 Genotype environment interaction

Based on the AMMI analysis, environment (E) was the major source of variability, indicating a large difference among environmental means causing variation in grain yield per plot. This implies that grain yields were significantly affected by E, accounting for 55.22% of the total variation, whereas G accounted for 27.46% and GxE for 17.44%. A previous report on wheat by Atinkut et al. (2022) also indicated that the environmental effects accounted for the largest proportion of the total variation, with environments accounting for 54% of the total variation, followed by the GEI (23%), whereas the genotype accounted for 16%. The AMMI analysis studied by Berhanu et al. (2022) showed that bread wheat grain yield was significantly affected by the environment, which explained 82.44% of the total variation. Comparatively, genotype and GEI captured 6.23% and 11.33% of the total variation, respectively. This implies existence of high variability among the studied environments.

4.3 Virulence variability of Ethiopian *P. striiformis* isolates and seedling resistance in bread wheat genotypes

4.3.1 Result

4.3.1.1 Combined analysis of variance

Data analysis on disease severity, seedling response, and coefficient of infection revealed very highly significant ($p=0.001$) variations among wheat genotypes, isolates, and their two-way interactions (Table 25). A considerable degree of virulence variability was found among the Ethiopian *P. striiformis* isolates, diversity among them being the primary source of variation (ANOVA, $P<0.01$). Furthermore, genotype specificity and pathogenicity variability among isolates were proposed. Disease severity, seedling response, and coefficient of infection varied significantly across the investigated wheat genotypes. Among the isolates' studied for their aggressiveness, isolate 4 was determined to be the most aggressive, with a mean disease severity of 3.16, a seedling response of 0.3, and a coefficient of infection of 0.95. With a mean disease severity of 2.60, seedling responses of 0.26, and an infection coefficient of 0.68, isolate 2 ranked second. Isolate 3, on the other hand, was found to be the least aggressive isolate, with a mean disease severity seedling response of 0.21 and 0.44, respectively (Supplemental Table 5).

Table 25. Summary of ANOVA for disease severity, seedling response and coefficient of infection on 178 bread wheat genotypes

Source of Variations	Degree of freedom	Mean Square		
		DS	SR	CI
Genotype (G)	167	1.13***	1.51***	0.01***
Isolate (I)	3	6.07***	6.37***	0.07***
Genotype*Isolate (G*I)	501	0.22***	0.22***	0.001***
R-square		0.86	0.86	0.83
Coefficient of variation (CV)		18.04	19.44	25.57
Grand mean		1.53	0.47	0.08

DS=disease severity, SR=seedling response, CI=coefficient of infection, *** = very highly significant ($p < 0.0001$), and DF = degree of freedom.

4.3.1.2 Virulence variability of Ethiopian *P. striiformis* isolates

The investigated *P. striiformis* isolates had very highly significant ($p=0.0001$) variable patterns of virulence on the evaluated bread wheat genotypes. *P. striiformis* isolates from Ethiopia were shown to be pathogenic on a wide range of wheat genotypes, with mean virulence ranging from 2.11 to 3.16. The percentages of immune, resistant, and intermediate genotypes in I1 (Deka isolate) were 11 (6.18%), 126 (70.79%), and 41

(94.44%), respectively. Similarly, in I2 (Hdasia isolate), seven (3.93%), 127 (71.35%), 43 (42.16%), and one (0.56%), genotypes were immune, resistant, intermediates, and susceptible, in the given order. Likewise, in I3 (Meraro isolate), 13 (7.3%), 136 (76.4%), 27 (15.17%), and 2 (1.12%) of the genotypes tested were immune, resistant, intermediates, and susceptible, respectively. The immune, resistant, intermediate, and susceptible genotypes in the I4 (Senatia isolate) were 4 (2.25%), 96 (53.92%), 71 (39.89%), and 7 (3.93%), respectively. The number of, resistant, intermediate, and susceptible genotypes immune to two or more isolates were, 4 (2.25%), 96 (53.92%), 27, and 1 (0.56%), respectively (Supplemental Table 5, Figure 23). G84, G93, G177, and Yr15 were the four immune genotypes containing two or more isolates.

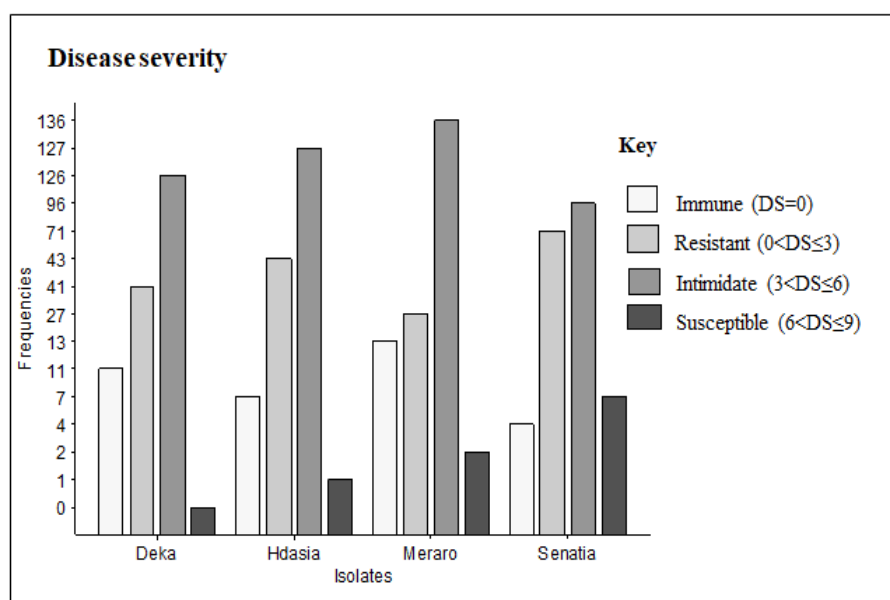


Figure 23. Disease Severity (DS) of 178 bread wheat genotypes to yellow rust, clustering involved Immune=0, resistant ($0 < DS \leq 3$), intermediate ($3 < DS \leq 6$) and susceptible ($6 < DS \leq 9$)

The seedling responses of the 178 bread wheat genotypes exposed to the four Pst isolates showed high variations. Figure 24 shows the total number and proportion of bread wheat genotypes belonging to various resistance classes. Forty three (24.16%), 125 (70.79%), and 10 (2.62%) of the genotypes in I1 were immune, resistant, and intermediate, respectively. In I2, six (3.37%), 184 (71.91%), 43 (24.16%), and one (0.56%), genotypes were immune, resistant, intermediate, and susceptible, respectively. Likewise, in I3; 12 (6.74%), 138 (77.53%), 26 (14.61%), and 2 (1.12%) of the genotypes were immune, resistant, intermediate, and susceptible, respectively. In I4, six genotypes (3.37%), 100 (56.18%), 65 (36.52%), and seven (3.93%) were immune,

resistant, intermediate, and susceptible. The majority of the genotypes were immune, resistant, intermediate, and susceptible to two or more isolates, with 6 (3.37%), 100 (56.18%), 26, (14.61%), and 1 (0.56%), respectively (Supplemental Table 3, Figure 24). The six isolates that were immune to two or more of the isolates were G84, G85, G93, G126, G173, and Yr15.

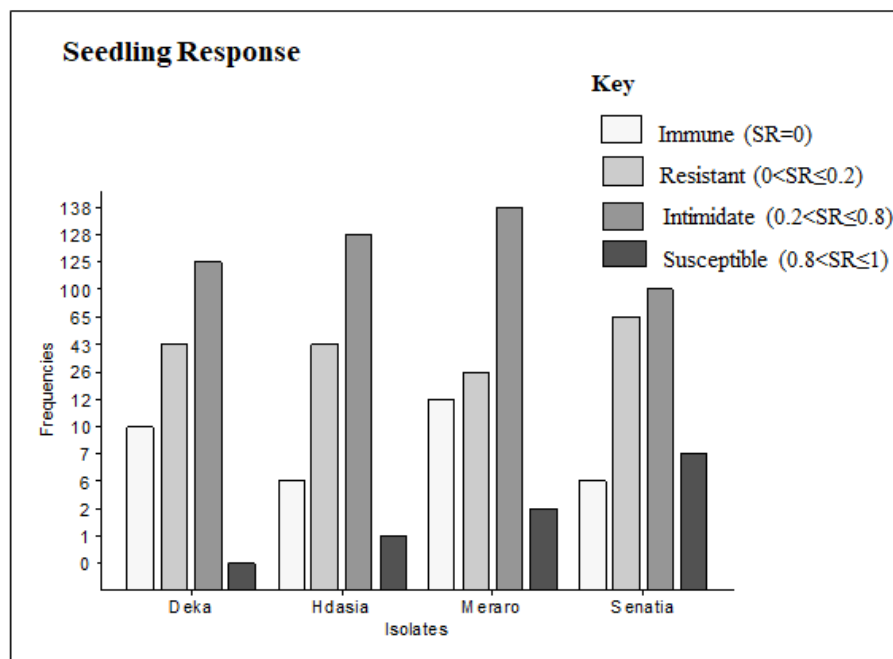


Figure 24. Seedling reaction response (SR) of 178 bread wheat genotypes to yellow rust Immune=0, resistant ($0 < SR \leq 0.2$), intermediate ($0.2 < SR \leq 0.8$) and susceptible ($0.8 < SR \leq 1$) groups.

In the same way, Figure 25 summarizes the coefficient of infection number and proportion of bread wheat germplasm in different resistance classes across the four isolates. In I1, nine (5.06%), 138 (77.53%), and 31 (17.42%) genotypes were immune, resistant, and intermediate, respectively. In I2, 4 (2.25%), 136 (76.4%), 36 (20.22%), and 2 (1.12%), were Immune, resistant, intermediate, and susceptible genotypes, respectively. Likewise, in I3 genotypes that were immune were 12 (6.74%), resistant 144 (80.89%), and intermediate 22 (12.36%). Also, I4 contained four (2.25%), 135 (75.84%), 38 (21.38%), and one (0.56%) immune, resistant, and intermediate genotypes, respectively. What's more, four (2.25%), 136 (76.4%), 22, (12.36%), and 0.56% of the genotypes were immune, resistant, or intermediate to two or more isolates (Supplemental Table 3, Figure 25). G84, G126, G177, and Yr15 were the four genotypes that were resistant to two or more isolates.

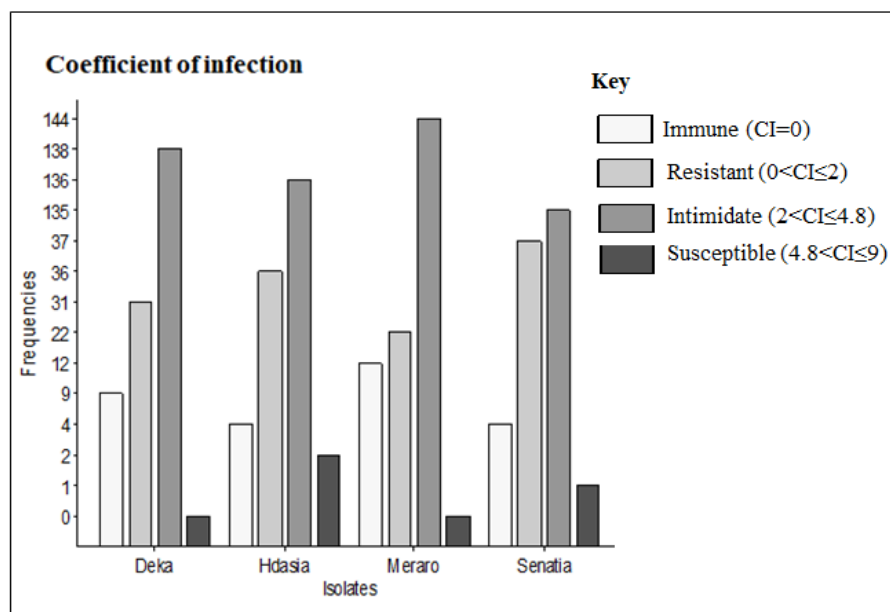


Figure 25. CI of yellow rust for 178 bread wheat genotypes obtained from greenhouse experiments in two replications. The genotypes were clustered as resistant ($0 < CI \leq 2$), intermediate ($2 < CI \leq 4.8$), susceptible ($4.8 < CI \leq 9$).

4.3.1.3 Differential lines resistance responses to Ethiopian *P. striiformis* isolates

According to race analysis on differential lines carrying mapped Yr genes, Ethiopian *P. striiformis* isolates exhibited great diversity in infection behavior. The differential line response analysis for disease severity, seedling response, and coefficient of infection to I1 was 0-3.5, 0-0.55, and 0-1.65, respectively. Furthermore, Coatez Yr15 and Avocet Yr9, which possesses Yr15 and Yr9, respectively, were immune to I1. Additionally, Avocet Yr9 resistance was isolate specific; nevertheless, Coatez Yr15 resistance was immune to all isolates. Also, Moro Yr10 and Yrs18, were immune to two (I2, I3) and three (I2, I3, I4) isolates, respectively. Differential lines Chines 166 and Lee, on the other hand, showed no immunological response to all isolates. In addition, susceptibility test "Morocco" confirmed that it was susceptible to all isolates. Proportion of divergent line wheat genotypes in disease severity, seedling response, and infection coefficient across all isolates is summarized in Table 26.

Table 26. Differential lines with known yellow (Yr) genes response to four *P. striiformis* isolates

Differential lines	Gene (s)	I1			I2			I3			I4		
		DS	SR	CI	DS	SR	CI	DS	SR	CI	DS	SR	CI
Moro Yr10	Yr10	2.5	0.4	1	0	0	0	0	0	0	1	0.15	0.15
Chines 166	Yr1	3	0.4	1.2	1	0.4	0.4	2.5	0.3	0.75	1.5	0.25	0.38
Coatez Yr15	Yr15	0	0	0	0	0	0	0	0	0	0	0	0
Yrs, 18	Yr18	1.5	0.15	0.23	0	0	0	0	0	0	0	0	0
Avocet Yr8+	Yr8+	3	0.55	1.65	1.5	0.15	0.23	0	0	0	2	0.25	0.5
Avocet Yr9	Yr9	0	0	0	1.5	0.55	0.83	1.5	0.1	0.15	1	0.15	0.15
Haybrid 46	Yr4	2	0.5	1	1.5	0	0	0	0.05	0.03	0	0	0
Kalinsana	Yr7	1.5	0.15	0.23	2.5	0.5	1.25	0	0	0	0.5	0.05	0.03
Lee	Yr7	3.5	0.4	1.4	1	0.15	0.15	3	0.2	0.6	1	0.15	0.15
Avocet	Yr8	3	0.4	1.2	0.5	0.4	0.2	0	0	0	0	0	0

I1=Deka isolate, I2= Hdasia isolate, I3=Meraro isolate, I4= Senatia isolate, DS=disease severity, SR=seedling response, CI=coefficient of infection

4.3.1.4 Cultivars resistance responses to Ethiopian *P. striiformis* isolates

Based on disease severity analysis results, I1 was shown to be virulent to Medawolabu, Meraro, Bika, and KI6295-4A, which carry *Yr4*, *Yr7*, *Yr8+*, *Yr10*, *Yr15*, *Yr18*; *Yr1*, *Yr7*, *Yr8*, *Yr9*; *Yr1*, *Yr8+*, *Yr8*, and *Yr1,Yr4,Yr8*, respectively. The investigation also found that Medawolabu and Paven-76 were moderately susceptible to I4. Yet, Bika did not provide resistance to any of the four tested isolates (Table 27 and 28). Based on the seedling response analysis results, cultivars that displayed an immune response were King Bird (possess *Yr1*, *Yr8*, *Yr9*, and *Yr15*) and Paven-76 (possess *Yr15*, *Yr9*, *Yr7*, and *Yr8*) to I1; Bika (possess *Yr4*, *Yr10*, and *Yr18*) to I2; Hoggena (possess *Yr4*, *Yr7*, *Yr8*, *Yr8+*, *Yr10*, *Yr15*, and *Yr18*); Medawolabu (possess *Yr4*, *Yr7*, *Yr8*, *Yr8+*, *Yr10*, *Yr15*, and *Yr18*) and K-6290-Bulk (possess *Yr10*, *Yr15*, *Yr18*, *Yr7*, and *Yr8*) to I3; and Sofomor (possess *Yr4*, *Yr7*, *Yr8*, *Yr15*, and *Yr18*) to I4. Besides, coefficient of infection data showed that King Bird (possess *Yr* and *Yr18*) and Paven-76 (possess *Yr1*, *Yr8+*, *Yr7*, and *Yr8*) were immune to I1. Bika possessed *Yr4*, *Yr10*, *Yr15* and *Yr18* were immune to I2. Hoggena (possess *Yr7*, *Yr8*, *Yr8+*, *Yr10*, *Yr15*, and *Yr18*), Medawolabu (possess *Yr7*, *Yr8*, *Yr8+*, *Yr10*, *Yr15*, and *Yr18*) and K-6290-Bulk (possess *Yr7*, *Yr8*, *Yr15*, *Yr18*, and *Yr4*) were immune to I3. Also, Sofomor possessed *Yr4*, *Yr8*, *Yr15*, and *Yr18* were immune to I4).

Table 27. Seedling reaction of 12 varieties to four Ethiopian isolates of *P. striiformis*

Disease severity					
Varieties	I1	I2	I3	I4	Postulated Yr genes
Et-13 A2 (G10)	2	2.5	2	2.5	<i>Yr4</i> , <i>Yr7</i>
Meraro (G14)	3	2.5	1.5	2.5	<i>Yr1</i> , <i>Yr8</i> , <i>Yr7</i> , <i>Yr9</i>
Alidoro (G21)	2.5	1.5	2	1.5	<i>Yr10</i> , <i>Yr9</i> , <i>Yr4</i> , <i>Yr8+</i> , <i>Yr1</i>
Hulukaka (G22)	0.5	1.5	1	1.5	<i>Yr9</i> , <i>Yr4</i> , <i>Yr8+</i> , <i>Yr1</i>
King Bird (G33)	2	3.5	0	4	<i>Yr4</i> , <i>Yr7</i> , <i>Yr8+</i>
Hoggena (G40)	2.5	2.5	1.5	2	<i>Yr4</i> , <i>Yr10</i> , <i>Yr8</i> , <i>Yr7</i> , <i>Yr9</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Bika (G80)	3	4.5	4.5	4.5	<i>Yr1</i> , <i>Yr8+</i> , <i>Yr8</i>
Medawolabu (G127)	5	2.5	0	5.5	<i>Yr4</i> , <i>Yr7</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Paven-76 (G149)	2	1.5	1	4.5	<i>Yr4</i> , <i>Yr9</i> , <i>Yr8+</i>
Sofomor (G152)	0.5	0.5	0.5	2.5	<i>Yr8</i>
K-6290-Bulk (G173)	2.5	1	0	0.5	<i>Yr10</i> , <i>Yr1</i> , <i>Yr7</i>
KI6295-4A (G175)	3	2	0.5	1.5	<i>Yr1</i> , <i>Yr8</i> , <i>Yr4</i>
Seedling response					
Varieties	I1	I2	I3	I4	Postulated Yr genes

Et-13 A2 (G10)	0.25	0.25	0.2	0.55	<i>Yr8+</i> , <i>Yr7</i>
Meraro (G14)	0.3	0.25	0.2	0.65	<i>Yr8+</i> , <i>Yr7</i>
Alidoro (G21)	0.25	0.2	0.3	0.15	<i>Yr1</i> , <i>Yr9</i> , <i>Yr7</i> , <i>Yr10</i>
Huluka (G22)	0.5	0.15	0.15	0.15	<i>Yr1</i> , <i>Yr4</i> , <i>Yr7</i> , <i>Yr8+</i> , <i>Yr9</i> , <i>Yr10</i> ,
King Bird (G33)	0	0.4	0.3	0.4	<i>Yr1</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr15</i>
Hoggena (G40)	0.25	0.3	0	0.3	<i>Yr4</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Bika (G80)	0.1	0	0.5	0.5	<i>Yr4</i> , <i>Yr10</i> , <i>Yr18</i>
Medawolabu (G127)	0.5	0.35	0	0.6	<i>Yr4</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Paven-76 (G149)	0	0.25	0.2	0.45	<i>Yr15</i> , <i>Yr9</i> , <i>Yr7</i> , <i>Yr8</i>
Sofomor (G152)	0.5	0.5	0.5	0	<i>Yr4</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr15</i> , <i>Yr18</i>
K-6290-Bulk (G173)	0.25	0.2	0	0.05	<i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i> , <i>Yr7</i> , <i>Yr8</i>
KI6295-4A (G175)	0.4	0.2	0.1	0.15	<i>Yr10</i> , <i>Yr1</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i>
Coefficient of infection					
Varieties	I1	I2	I3	I4	Postulated Yr genes
Et-13 A2 (G10)	0.63	0.5	0.4	1.375	<i>Yr7</i>
Meraro (G14)	0.9	0.625	0.3	1.625	<i>Yr18</i>
Alidoro (G21)	0.625	0.3	0.6	0.225	<i>Yr7</i>
Huluka (G22)	0.25	0.23	0.15	0.225	<i>Yr18</i> , <i>Yr4</i> , <i>Yr8+</i>
King Bird (G33)	0	1.4	0.45	1.6	<i>Yr1</i> , <i>Yr8+</i>
Hoggena (G40)	0.63	0.75	0	0.6	<i>Yr7</i> , <i>Yr8</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Bika (G80)	0.3	0	2.25	2.25	<i>Yr4</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Medawolabu (G127)	2.5	0.88	0	3.3	<i>Yr7</i> , <i>Yr8</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Paven-76 (G149)	0	0.375	0.2	2.025	<i>Yr1</i> , <i>Yr8+</i> , <i>Yr7</i> , <i>Yr8</i>
Sofomor (G152)	0.25	0.25	0.25	0	<i>Yr4</i> , <i>Yr8</i> , <i>Yr15</i> , <i>Yr18</i>
K-6290-Bulk (G173)	0.63	0.2	0	0.025	<i>Yr7</i> , <i>Yr8</i> , <i>Yr1</i> , <i>Yr15</i> , <i>Yr18</i> , <i>Yr4</i>
KI6295-4A (G175)	1.2	0.4	0.05	0.225	<i>Yr10</i> , <i>Yr7</i> , <i>Yr8</i>

Table 28. Stable Yr genes of 8 varieties in four Ethiopian isolates of *P. striiformis*

Varieties	Stable Yr genes
Et-13 A2 (G10)	<i>Yr7</i>
Huluka (G22)	<i>Yr4</i> , <i>Yr8+</i>
King Bird (G33)	<i>Yr8+</i>
Hoggena (G40)	<i>Yr7</i> , <i>Yr8</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Medawolabu (G127)	<i>Yr7</i> , <i>Yr8+</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr18</i>
Paven-76 (G149)	<i>Yr8+</i>
Sofomor (G152)	<i>Yr8</i>
KI6295-4A (G175)	<i>Yr8</i>

4.3.1.5 Cluster analysis of the wheat genotypes

The coefficients of infection of 178 bread wheat genotypes was categorized into three clusters using hierarchical cluster analysis (Supplementary Table 3). Cluster I contained genotypes resistant to all examined Ethiopian *P. striiformis* isolates. In cluster I, the mean coefficient of infection ranges from 0.13% (G126) to 2.99% (G31), with an overall mean of 1.38. Around 72.5% of the genotypes in this cluster had mean coefficient of infection values higher than the cluster mean, whereas 27.5% had coefficient of infection values lower than the group mean. Similarly, cluster II contained 11 (6.18%) genotypes that demonstrated two to three isolate-specific resistance reactions to the tested Ethiopian *P. striiformis* isolates. In this cluster, the mean coefficient of infection ranged from 0.81 (G119) to 2.08 (G172), with an overall mean of 1.25. Approximately 45.5% of the genotypes in this cluster had mean severity values greater than the cluster mean, whereas the remaining 54.5% had coefficient of infection values lower than the group mean. In addition, cluster III, which contained 126 genotypes (70.79%), exhibited a mean coefficient of infection ranging from 0 (G183) to 2.66 (G29), with an overall mean of 1.35. About 61.9% of the genotypes in this cluster had mean severity values greater than the cluster mean, whereas the remaining 38.1% of the germplasm had coefficient infection values lower than the group mean. Cluster III contained 66.66 diverse lines and commercial cultivars (G14, G22, G40, G80, G127, G147, G152, and G173). Germplasm G30 was one of the three groups that were not isolate-specific and resistant to all of the examined isolates (Figure 26).

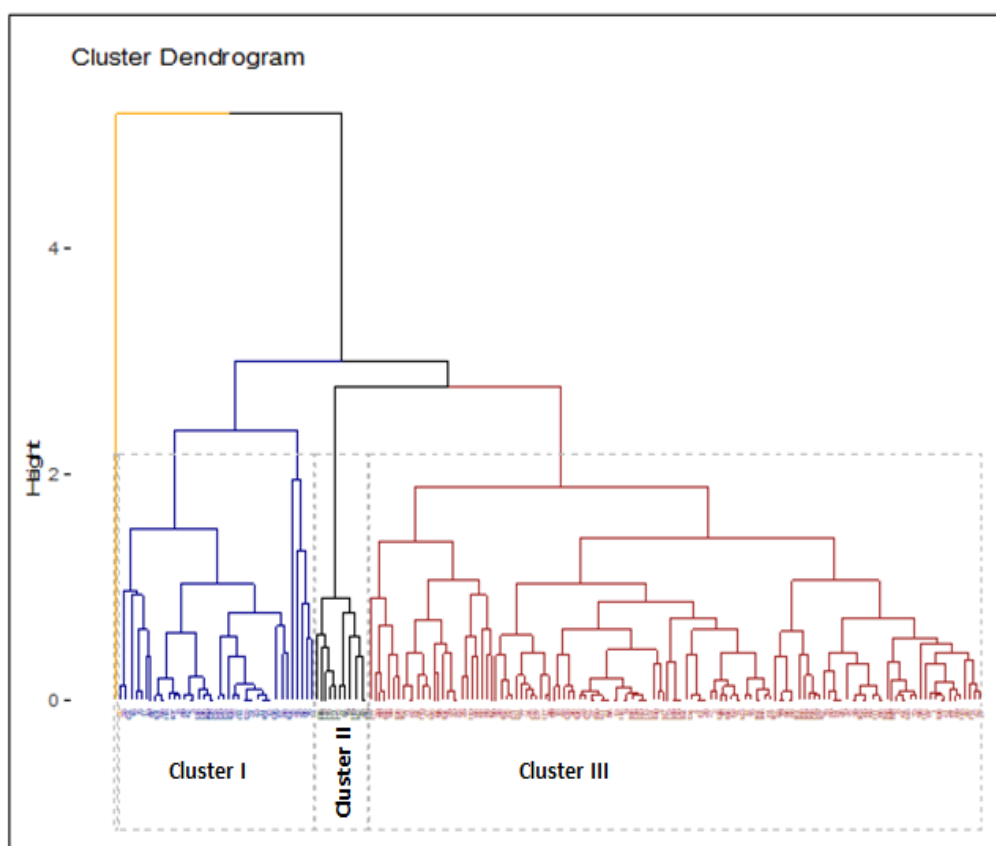


Figure 26. Dendrogram based on hierarchical cluster analysis of 178 bread wheat genotypes generated by four *P. striiformis* isolates under greenhouse conditions. The node positions correspond to Euclidian distances on the top horizontal axis. Using R-software, the dendrogram was generated using the average linkage hierarchical clustering algorithm and Euclidean distance (R Core Team 2020).

4.3.2 Discussion

The virulence pattern of four stripe rust isolates collected from main wheat growing areas of Ethiopia was examined 178 genotypes at the seedling stage, with disease severity, seedling response, and coefficient of infection all taken into account. The interaction effect was shown to be very highly significant ($p=0.0001$) in the combined analysis of variance for disease severity, seedling response, and coefficient of infection, demonstrating the presence of variable interactions in the tested isolates. It demonstrated the presence of cultivar specificity as well as virulence variation among Ethiopian stripe rust isolates. Out of the studied wheat genotypes 78.65% have shown significant resistance responses to one or more *P. striiformis* isolates. Among the wheat genotypes studied, 4 (2.25%) and 136 (76.4%) demonstrated immune and resistant responses to one or more *P. striiformis* isolates, respectively. The other 38 (21.35%) wheat genotypes included in this study showed no isolate-specific resistance response and were vulnerable to one or more *P. striiformis* isolates examined. As a result, these

genotypes are unlikely to be viable sources of resistance genes against Ethiopian *P. striiformis* populations.

Moreover, this study indicated that the examined stripe rust isolates had a considerable level of aggressiveness and variability. Isolate I4 was found to be the most aggressive, with a mean DS (3.16), SR (0.3), and CI (0.95). On the other side, I3 was detected to be the least aggressive with a mean value of DS (2.11), SR (0.21), and CI (0.44), indicating that it may have an avirulence gene that is recognized by a common resistance gene. This analysis on wheat germplasm demonstrated that tested Ethiopian *P. striiformis* isolates had a considerable variation in virulence patterns. Mercy et al., (2019) discovered significant virulence variations across 65 Kenyan wheat germplasm evaluated on 12 isolates. Similarly, the current study confirmed that Ethiopian stripe rust isolates have broad-spectrum virulence and a considerable level of aggressiveness, implying the need for a gene management strategy that incorporates a combination of genes (gene pyramiding) that can provide adequate protection and long-term control of stripe rust in the country. Furthermore, the comparatively highly virulent isolates (I4) found in this study can be exploited in wheat resistance breeding.

According to Yr gene efficacy study, Ethiopian stripe rust isolates had considerably diverse virulence patterns on the examined Yr genes. Accordingly, isolate I1 was shown to be the most virulent isolate causing stripe rust on Moro, Chines 166, Yrs 18, Avocet Yr8+, Haybrid 46, Kalinsana, Lee, and Avocet that carry the resistance genes *Yr10*, *Yr1*, *Yr18*, *Yr8+*, *Yr4*, *Yr7*, *Yr7*, and *Yr8*, respectively. This shows that more research into other Yr genes, gene pyramiding, and adult plant resistance is required. The differential lines Lee (carrying *Yr7*) and Chines 166 (carrying *Yr10*), on the other hand, did not show immune response to any Ethiopian stripe rust isolates, implying that they are not reliable sources of significant resistance genes. Similarly, Mercy et al., (2019) observed that Lee is susceptible to all tested isolates however Chines 166 (carrying *Yr10*) was reported as immune. Yr15, on the other hand, was observed as resistant to a diverse spectrum of yellow rust isolates from various geographical regions (Dubin et al., 1989; Mercy et al., 2019). Furthermore, three genotypes (Moro *Yr10*, Coatez *Yr15*, and Yrs, 18) showed immune responses to three Ethiopian *P. striiformis* isolates, implying that these genotypes could be proper source of significant resistance.

Among the tested released wheat varieties, Bika did not exhibit resistance to any of the assessed *P. striiformis* populations except to I2, implying that it may not be the appropriate genotype for growing in severe stripe rust outbreaks, even if it has other desirable agronomic characteristics. Commercial cultivars Paven-76, Et-13 A2, Meraro, Alidoro, Huluka Sofomor, Hoggena, KI6295-4A and KI6295-4A showed disease severity immune to resistant (0 to 2.5) responses to all tested isolates. This indicates that most wheat cultivars in Ethiopia were selected for other stress resistances despite their widespread cultivation in stripe rust hot spot areas. Moreover, all commercial cultivars except Buka and Medawolabu showed coefficient of infection immune to resistant (0 to 2) responses to all tested isolates. This reveals that these genotypes could be good sources of major resistance genes against stripe rust as well as appropriate genotypes for growing in stripe rust hot spots areas of Ethiopia. Based on coefficient of infection responses many commercial cultivars Hoggena, Bika, Medawolabu, Sofomor and K-6290-Bulk have Yr15 plus other genes. In which, Yr15 was reported as full stage resistance that was discovered in 25 Iranian wheat lines (Xiaodan et al., 2011). Based on the mean coefficient of infection, genotypes with reasonably broad-spectrum resistance were clustered into the same cluster (Cluster III), indicating that genotypes in this cluster could be good sources of resistance genes for enhancing bread wheat resistance to stripe rust. Overall, the study confirmed that commercial cultivars Et-13 A2, Huluka, King Bird, Hoggena, Medawolabu, Paven-76, Sofomor, and KI6295-4A contained a total of seven stable Yr genes, which demonstrated the highest level of resistance to Ethiopian *P. striiformis* isolates and thus could be the best sources of resistance for breeders looking to improve the resistance of Ethiopian bread wheat cultivars to stripe rust.

4.4 Genetic architecture of adult-plant stripe rust resistance in bread wheat genotypes association panel; GWAS

4.4.1 Result

4.2.1.1 Yellow rust infection and field response

The panel was divided into resistant, intermediate, and susceptible groups based on DS, FR, and CI data that were pooled from all growth stages and environments. The panel showed variable reaction groups for DS, FR, and CI. For DS, 65.73% of the genotypes were resistant ($0 \leq DS \leq 10$) at Hol (Holeta), 10.11% at Kul (Kulumsa), and 1.69% at Mer (Meraro) (Figure 27). With regard to FR, 96.6% of the genotypes joined the resistant

group at Holeta, 50.56% at Kulumsa, and 6.74% at Meraro (Figure 28). Likewise, for CI, 60.11%, 3.37%, and 1.12% of the wheat genotypes tested were resistant at the Holetta, Kulumsa, and Meraro locations, respectively (Figure 28). Since CI is a combined representation of DS and FR (Liu et al., 2017), out of the 178 tested genotypes, clustering based on this parameter resulted in 5 stable resistant genotypes (2.81%), 119 intermediate genotypes (66.85%), and 54 susceptible genotypes (32.02%) (Figure 29).

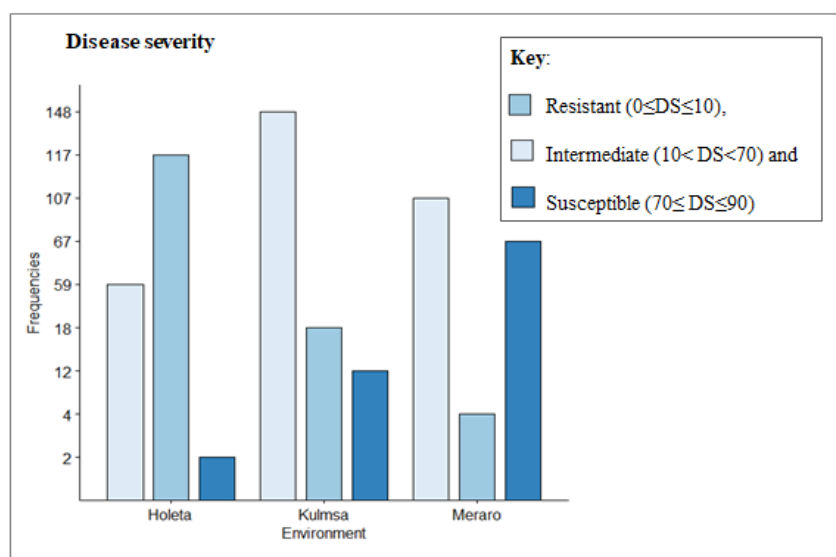


Figure 27. Yellow rust disease severity (DS) of 178 bread wheat genotypes at three locations, clustering involved resistant ($0 \leq DS \leq 10$), intermediate ($10 < DS < 70$), and susceptible ($70 \leq DS \leq 90$)

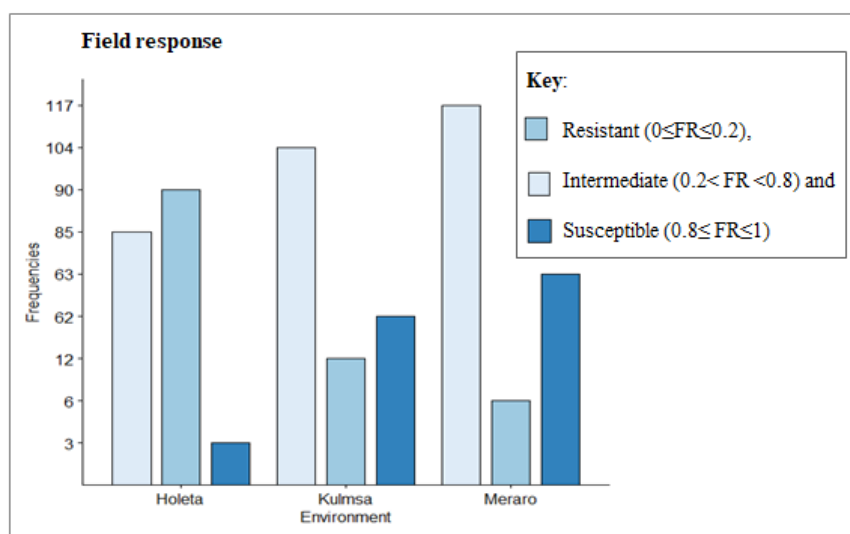


Figure 28. Field reaction response (FR) of 178 bread wheat genotypes to yellow rust resistant ($0 \leq FR \leq 0.2$), intermediate ($0.2 < FR < 0.8$), and susceptible ($0.8 \leq FR \leq 1$) groups

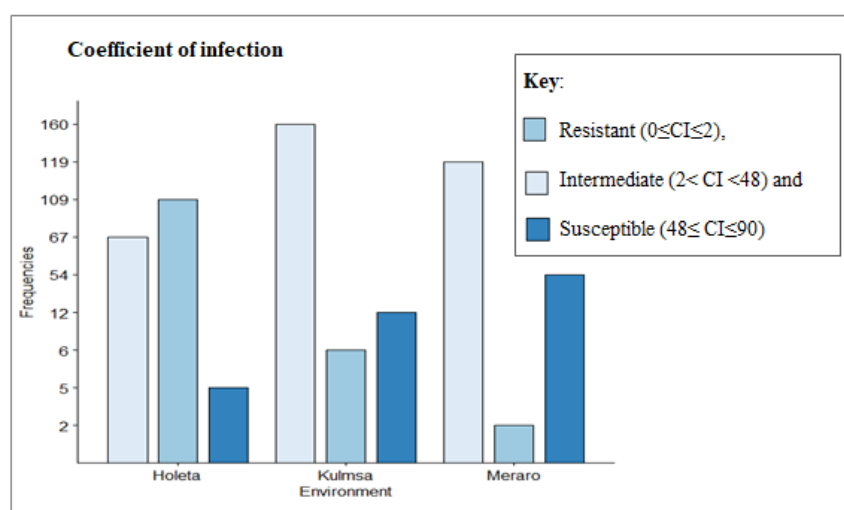
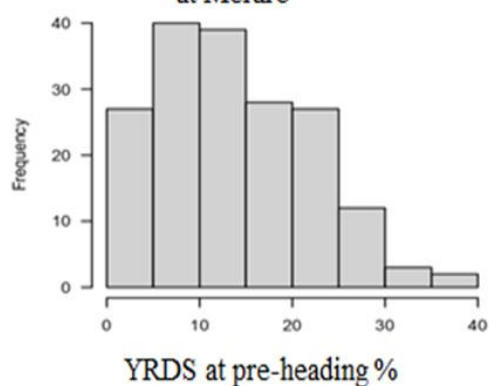


Figure 29. CI of yellow rust for 178 bread wheat genotypes obtained from field experiments in three environments. The genotypes were clustered as resistant ($0 \leq CI \leq 2$), intermediate ($2 < CI < 48$), and susceptible ($48 \leq CI \leq 90$).

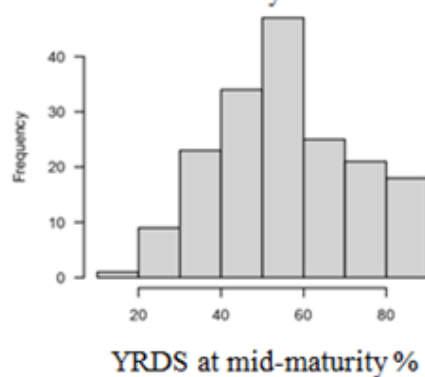
4.4.1.2 Adult-plant resistance to yellow rust and broad-sense heritability

Yellow rust coefficient of infection traits showed pseudo-normal distributions (Figure 30) in the investigated bread wheat genotype, indicating the quantitative nature of adult-plant yellow rust resistance. The genotypes' mean performance, standard deviations, range, and significance level for phenotypic traits considered for this study was measured in each environment. The genotypes showed very highly significant differences ($p < 0.001$) for measured traits in each and across environments, and at all growth stages. The analysis revealed that the coefficient of infection in each environment showed an increased trend from pre-heading (2.54-15.43%) to maturity stages (12.32 - 60.24%). The highest (60.24%) mean severity values were registered at Meraro at the maturity stage, while the lowest infestation severity (2.54%) was recorded at the pre-heading stage at Holeta. The pooled data revealed that the coefficient of infection was the highest at Meraro (43.34%), followed by Kulumsa (21.97%), and the lowest at Holeta (7.35%) (Table 29).

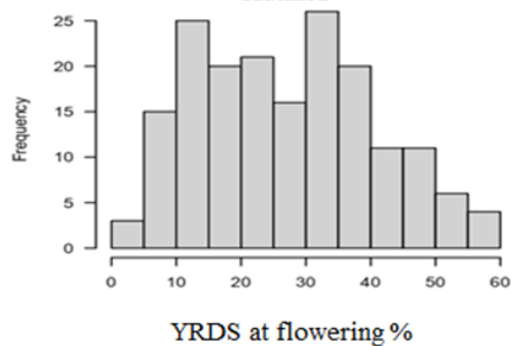
A) Yellow rust disease severity at pre-heading at Meraro



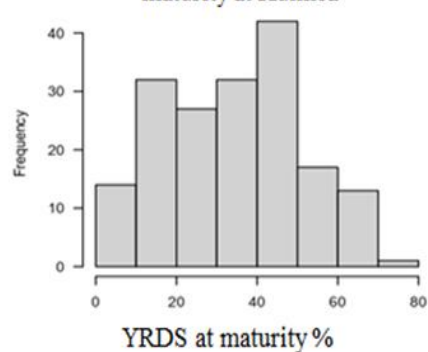
B) Yellow rust disease severity at mid-maturity at Meraro



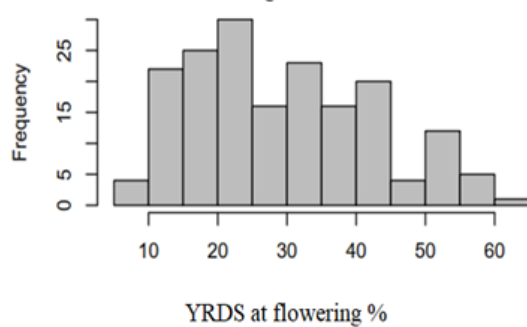
C) Yellow rust disease severity flowering at Kulmsa



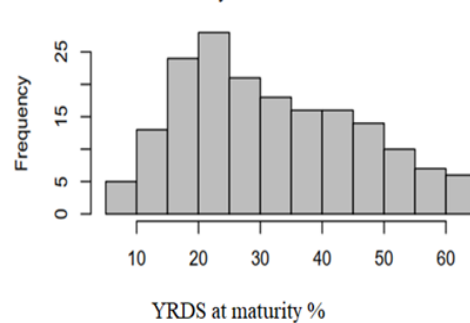
D) Yellow rust disease severity at maturity at Kulmsa



E) Yellow rust disease severity at flowering at Holeta



F) Yellow rust disease severity at maturity at Holeta



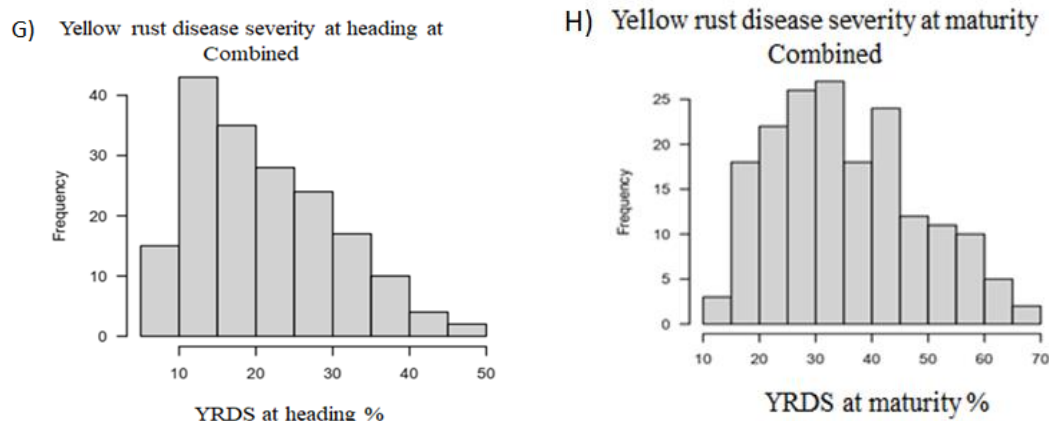


Figure 30. Frequency distribution of some yellow rust resistance traits for the combined data from three locations, the right and left ends of the bars indicate the uppermost and lowermost infection classes, respectively. The disease resistance at the pre-heading, heading, and mid-maturity stages followed a virtually pseudo-normal distribution. YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF= coefficient of infection at flowering, YRMM= coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity

Table 29. Mean range and standard deviation of five traits in three individual environments

Trait	Environment	Mean	Range	SD	Pr > F
YRPH	E2 (Kulumsa)	8.30	14.5	7.25	<.0001***
	E3(Meraro)	15.43	24	9.86	<.0001***
	E1 (Holeta)	4.66	24.5	10.39	<.0001***
YRH	E2 (Kulumsa)	22.69	33	10.94	<.0001***
	E3(Meraro)	36.06	71	13.8	<.0001***
	E1 (Holeta)	7.59	25.6	13.7	0.0001**
YRF	E2 (Kulumsa)	28.52	53	11.86	<.0001***
	E3(Meraro)	47.64	86	15.24	<.0001***
	E1 (Holeta)	9.64	25.5	15.44	<.0001***
YRMM	E2 (Kulumsa)	30.81	34	14.13	<.0001***
	E3(Meraro)	57.30	72.5	17.02	<.0001***
	E1 (Holeta)	12.32	25	30.45	0.0049*
YRM	E2 (Kulumsa)	19.51	22.5	7.22	<.0001***
	E3(Meraro)	60.24	67	17.2	<.0001***
	E1 (Holeta)	7.35	12.4	12.49	<.0001***

YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, SD = standard deviation, *** = very highly significant at $p < 0.0001$, ** = highly significant at $p < 0.001$, * = significant at $p < 0.05$

For the coefficient of infection, the combined ANOVA revealed that the effects of genotype, location, and their two-way interactions (genotype x location) were very highly significant ($p < 0.0001$) (Table 30). Moreover, blocking had a significant effect

on genotype performance for yellow rust resistance. The ANOVA using pooled data revealed that genotypic variance (σ^2_g) and environmental variation (σ^2_e) were the major sources of the variation for the coefficient of infection variability among the tested wheat genotypes. As per the scale of Robinson (1949), yellow rust resistance showed moderate broad sense heritability ($30\% \leq H^2 \leq 60\%$) in all individual environments except for the pre-heading stage, where the broad sense heritability was lower ($H^2=27.37\%$). Focusing on the coefficient of infection, the heritability in individual environments revealed that yellow rust resistance is highly heritable ($h^2 = 74.52\text{-}88.64\%$). The genetic and phenotypic coefficients of variation for variables related to the coefficient of infection ranged from 40.23% (YRMM) to 61.49% (YRPH) and 65.29% (YRMM) to 117.53% (YRPH), respectively (Table 30). At 5% selection intensity, the range of magnitude of the expected genetic gain as a percent of the mean varied from 48.76% (YRM) to 66.36% (YRPH), whereas the genetic advance for the coefficient of infection ranged from 5.81 (YRPH) to 16.66 (YRMM) (Table 31).

Table 30. Combined ANOVA for yellow rust coefficient of infection

Source of variation	DF					
		YRPH	YRH	YRF	YRMM	YRM
Genotype	17	242.52***	707.82***	1051.76***	1288.05***	1325.01***
	7					
Replication	1	1322.25***	0.13 ^{ns}	217.80 ^{ns}	176.42 ^{ns}	163.18 ^{ns}
Incomplete block	5	177.54***	564.62***	647.87***	652.17***	704.71*
Location	2	15013.82***	89355.23***	144498.68***	205404.21***	240403.97***
Genotype*	35					
location	8	85.28*	209.20**	274.82**	303.67*	541.58**

YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, *** = very highly significant at $p < 0.001$, ** = highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

Table 31. Variance components, heritability, and genetic advances of coefficient of infection traits of 178 wheat genotypes based on pooled data from three environments.

Trait	σ^2_g	σ^2_e	σ^2_p	PCV	GCV	H^2	h^2	GA	GAM
YRPH	85.28***	68.59***	6.49***	117.53	61.49	27.37	81.47	5.81	66.36
YRH	209.20***	156.36***	13.44***	78.41	45.36	33.46	84.01	11.44	54.12
YRF	274.82***	213.39***	13.44***	70.18	42.34	36.40	86.35	14.71	52.71
YRMM	303.67***	257.31***	8.79***	65.27	40.23	37.98	88.64	16.66	51.15
YRM	541.58***	273.88***	8.89***	78.65	43.12	30.05	74.54	14.97	48.76
Average				79.73	45.93	34.15	83.83	12.85	54.83

YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, σ^2_g = Genotypic variance estimate, σ^2_p = phenotype variance estimate, σ^2_e = residual variance estimate, GCV = Genotypic coefficient of variance, PCV = Phenotypic coefficient of variance, GA = Genetic advance, H^2 = broad sense heritability, h^2 = narrow sense heritability, GAM = Genetic advance as percent mean (GAM), *** = very highly significant at $p < 0.001$

Using comparative resistance analysis with the standard check Kingbird (G40), and the average performance of the released varieties, among the investigated materials, there were superior genotypes with yellow rust resistance. Among the 178 genotypes examined, 106 (60.57%) genotypes at pre-heading, 38 (19.66%) genotypes at heading, 120 (67.42%) at flowering, 123 (60.16%) at mid-maturity, and 132 (74.16%) at maturity stage exhibited quantitatively superior yellow rust resistance as compared to the standard check Kingbird (Table 32, Supplementary Table 4). The top 5% best genotypes had 82.21%-100% greater resistance at pre-heading, 55.27%-73.16% at heading, 57.26%-80.70% at flowering, 61.11%-72.65% at mid-maturity, and 61.34%-75.46% greater resistance at maturity stage compared to the mean performance of the Kingbird. Furthermore, the top 5% of the best genotypes had 80.53%-100% greater resistance at pre-heading, 67.95%-80.77% at heading, 69%-86% at flowering, 47.70%-63.22% at mid-maturity and 71.70%-82.04% at maturity stage, according to the average performance of the released varieties.

Table 32. Comparison of top 5% of the selected genotypes for Yr resistance with KB, and mean performances of 13 released varieties.

Gen	Mean of selected genotypes at YRPH	Comparative advantage for Yr resistance (% over)		Gen	Mean of selected genotypes at YRH	Comparative advantage for Yr resistance (% over)	
		KB	MRV*			KB	MRV*
G28	0.00	100.00	100.00	G171	5.00	73.16	80.77
G32	0.00	100.00	100.00	G176	5.00	73.16	80.77
G74	0.00	100.00	100.00	G93	6.00	67.79	76.92
G90	0.00	100.00	100.00	G125	6.17	66.90	76.28
G34	1.00	89.66	88.32	G90	7.00	62.43	73.08
G133	1.33	86.21	84.42	G21	8.00	57.06	69.23
G3	1.67	82.76	80.53	G34	8.00	57.06	69.23
G38	1.67	82.76	80.53	G33	8.17	56.16	68.59
G39	1.67	82.76	80.53	G58	8.33	55.27	67.95
KB	9.67	--	-12.97	KB	18.63	--	28.35
MRV*	8.56	11.44	--	MRV*	26.00	-39.56	--
Gen	Mean of selected genotypes at YRF	Comparative advantage for Yr resistance (% over)		Gen	Mean of selected genotypes at YRMM	Comparative advantage for Yr resistance (% over)	
		KB	MRV*			KB	MRV*
G88	4.67	80.70	86.00	G93	10.67	72.65	63.22
G93	6.00	75.19	82.00	G176	11.00	71.79	62.07
G125	6.67	72.43	80.00	G33	13.00	66.67	55.17
G176	8.00	66.91	76.00	G125	13.33	65.81	54.02
G73	9.67	60.02	71.00	G38	14.00	64.10	51.72
G159	9.67	60.02	71.00	G79	14.17	63.68	51.15
G58	10.00	58.64	70.00	G81	14.67	62.39	49.43
G147	10.17	57.95	69.50	G150	14.67	62.39	49.43
G59	10.33	57.26	69.00	G147	15.17	61.11	47.70
KB	24.18	--	27.45	KB	39.00	--	-34.48
MRV*	33.33	-37.84	--	MRV*	29.00	25.64	--
Gen	Mean of selected genotypes At YRM	Comparative advantage for Yr resistance (% over)		Gen = Genotypes, Yr = yellow rust, KB =Kingbird, MRV* = Mean of 13 selected released varieties. Negative values for comparative advantage indicate less yellow rust resistance of the genotype. YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity.			
		KB	MRV*				
G93	11.00	75.46	82.04				
G176	13.00	71.00	78.78				
G38	14.00	68.77	77.14				
G147	15.17	66.17	75.24				
G150	15.67	65.05	74.42				
G125	15.83	64.68	74.15				
G33	16.33	63.57	73.33				
G79	17.00	62.08	72.24				
G55	17.33	61.34	71.70				
KB	44.83	--	26.80				
MRV*	61.25	-36.63	--				

Pearson's correlation analysis of important agronomic traits revealed a strong negative association of yellow rust resistance with the assessed traits. Spike length showed a non-significant, weak negative correlation with all yellow rust resistance traits except at the pre-heading stage, where the association was strongly negative. All the yellow rust resistance traits showed a strong negative correlation with leaf area, plant height, thousand kernel weight, and number of kernels per spike, spike weight, and grain yield. The yellow rust resistance traits showed a significant weak to moderate negative correlation with spike length and plant height (Table 33).

Table 33. Correlation analysis among disease severity, field response, coefficient of infection, and other agronomic traits at different plant stages

DS									
Traits	FD	MD	LA	PH	SL	TKW	NKS	SW	GY
YRPH	0.20**	-0.05 ^{ns}	-0.55**	-0.51***	-0.21***	-0.51***	-0.72***	-0.88***	-0.66***
YRH	0.20***	-0.06 ^{ns}	-0.48***	-0.51**	-0.14 ^{ns}	-0.48***	-0.63***	-0.78***	-0.60***
YRF	0.18*	0.004 ^{ns}	-0.45***	-0.50***	-0.07 ^{ns}	-0.51***	-0.63***	-0.88***	-0.66***
YRMM	0.17*	0.001 ^{ns}	-0.49***	-0.51***	-0.06 ^{ns}	-0.47***	-0.63***	-0.81***	-0.65***
YRM	0.13 ^{ns}	-0.02 ^{ns}	-0.50***	-0.52***	-0.55 ^{ns}	-0.47***	-0.64***	-0.81***	0.65**
FR									
traits	FD	MD	LA	PH	SL	TKW	NKS	SW	GY
YRPH	0.27**	-0.01 ^{ns}	-0.39**	-0.34***	-0.14**	-0.48***	-0.61***	-0.78**	-0.50***
YRH	0.54**	0.15*	-0.55***	-0.02 ^{ns}	-0.29 ^{ns}	-0.81***	-0.62***	-0.82***	-1.07***
YRF	0.10 ^{ns}	0.02 ^{ns}	-0.44***	-0.34**	-0.05 ^{ns}	-0.51**	-0.54***	-0.62***	-0.85**
YRMM	0.29**	0.16*	-0.55***	-0.42***	-0.10***	-0.67***	-0.67***	-0.82***	-1.02***
YRM	0.12 ^{ns}	-0.15	-0.37***	-0.60**	-0.08 ^{ns}	-0.75***	-0.70***	-0.72***	-0.77***
CI									
Traits	FD	MD	LA	PH	SL	TKW	NKS	SW	GY
YRPH	0.26***	-0.02 ^{ns}	-0.55**	-0.48***	-0.04 ^{ns}	0.80***	-0.73***	-0.89***	-0.68***
YRH	0.29***	-0.04 ^{ns}	-0.48**	-0.49***	-0.12 ^{ns}	-0.49***	-0.62***	-0.79***	-0.62***
YRF	0.23***	-0.01 ^{ns}	-0.50**	-0.48**	-0.09 ^{ns}	-0.51**	-0.65***	-0.80***	-0.67***
YRMM	0.23***	-0.01 ^{ns}	-0.54**	-0.50***	-0.10 ^{ns}	-0.50***	-0.67***	-0.83***	-0.71***
YRM	0.22***	-0.00 ^{ns}	-0.49**	-0.48**	-0.09 ^{ns}	-0.52***	-0.67***	-0.83***	0.68***

YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, FD = days to 50% flowering, MD= days to maturity, LA= leaf area, TKA= thousand kernel weight, NKS= number of kernels per spike, SW= spike weight, GY= grain yield, *** = very highly significant at $p < 0.001$, ** = highly significant at $p < 0.001$, * = significant at $p < 0.05$, ns = non-significant at $p = 0.05$ significance level

4.4.1.3 SNP Statistics

DArTSeq genotyping of the 178 bread wheat genotypes resulted in 35,672 SNPs. Among the three wheat sub-genomes, 10,317, 10,979, and 9,756 SNPs distributed on sub-genomes A, B, and D respectively (Figure 31). The highest (2184) number of SNPs

was found on chromosome 7A. While chromosome 4D contained the lowest (833) number of SNPs, After filtering of call rates > 70% and minor allele frequencies > 0.05, a total of 6,788 SNP markers were obtained out of which 2,410 SNPs were distributed on the A sub-genome, 2,872 on the B sub-genome and 1506 on the D sub-genome.

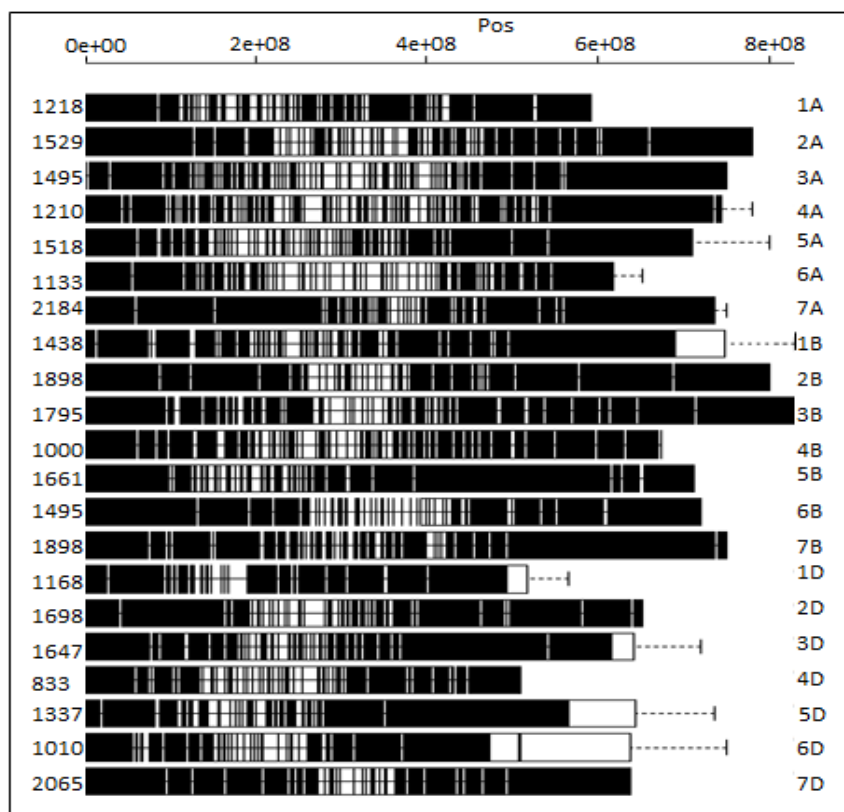


Figure 31. . Distribution of SNPs on 21 bread wheat chromosomes

3.4.1.4 Population structure analysis

Based on the output of the STRUCTURE software three sub-populations were inferred (Figure 32A). The three clusters (Figure 32B) showed a significant degree of genetic mixing, indicating that the studied wheat populations are closely related. All of the individual genotypes shared genes inherited from all three subpopulations. The scatter plot (Figure 33A) and 3D plot of the first three principal components (Figure 33B) confirmed the existence of three clusters in the association panel with greater admixture, where the first two PCs (PC1 and PC2) coordinates explained the majority of the variation. The presence of cryptic familiar relatedness was verified by kinship analysis (Figure 33C) demonstrating the significance of including both population structure (Q) and kinship (K) as covariates in marker-trait association analyses.

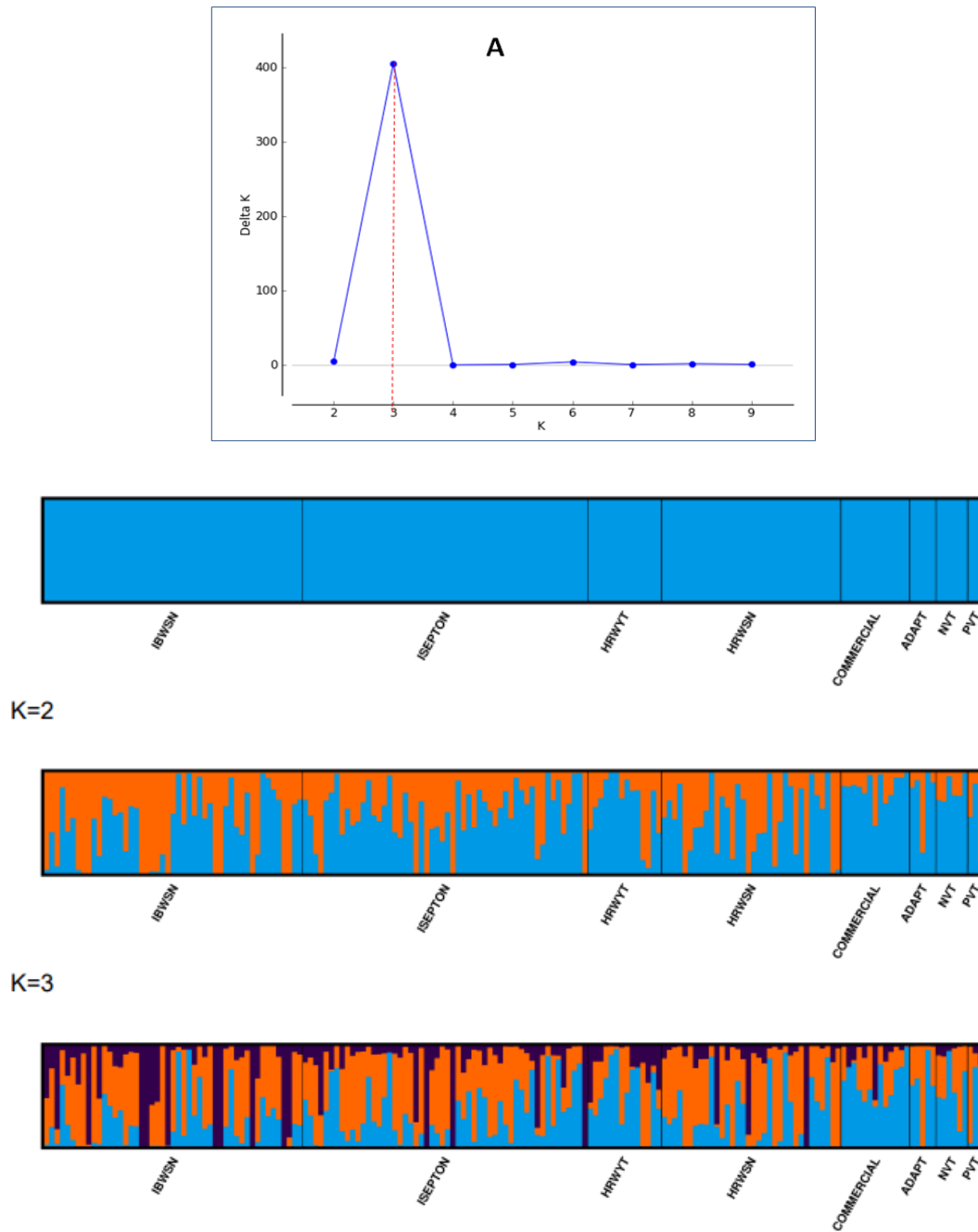


Figure 32. Population structures of 178 bread wheat genotypes representing eight populations. (A) Best delta K value estimated, and the pick at $k = 3$ indicates the number of sub-populations in the wheat panel. (B) Estimated population structure for $K = 3$ according to the breeding materials. The different colors (blue, orange, and black) represent genetic groups or sub-populations: the x-axis represents individual samples and the y-axis represents the proportion of ancestry to each cluster. Population abbreviations are IBWSN = International Bread Wheat Screening Nursery; ISEPTON = International Septoria Observation Nursery; HRWYT = High Rain Wheat Yield Trial; HRWSN = High Rain Wheat Screening Nursery; ADAPT = Adaptation trial; NVT = National variety trial; and PVT = Preliminary Verification trial.

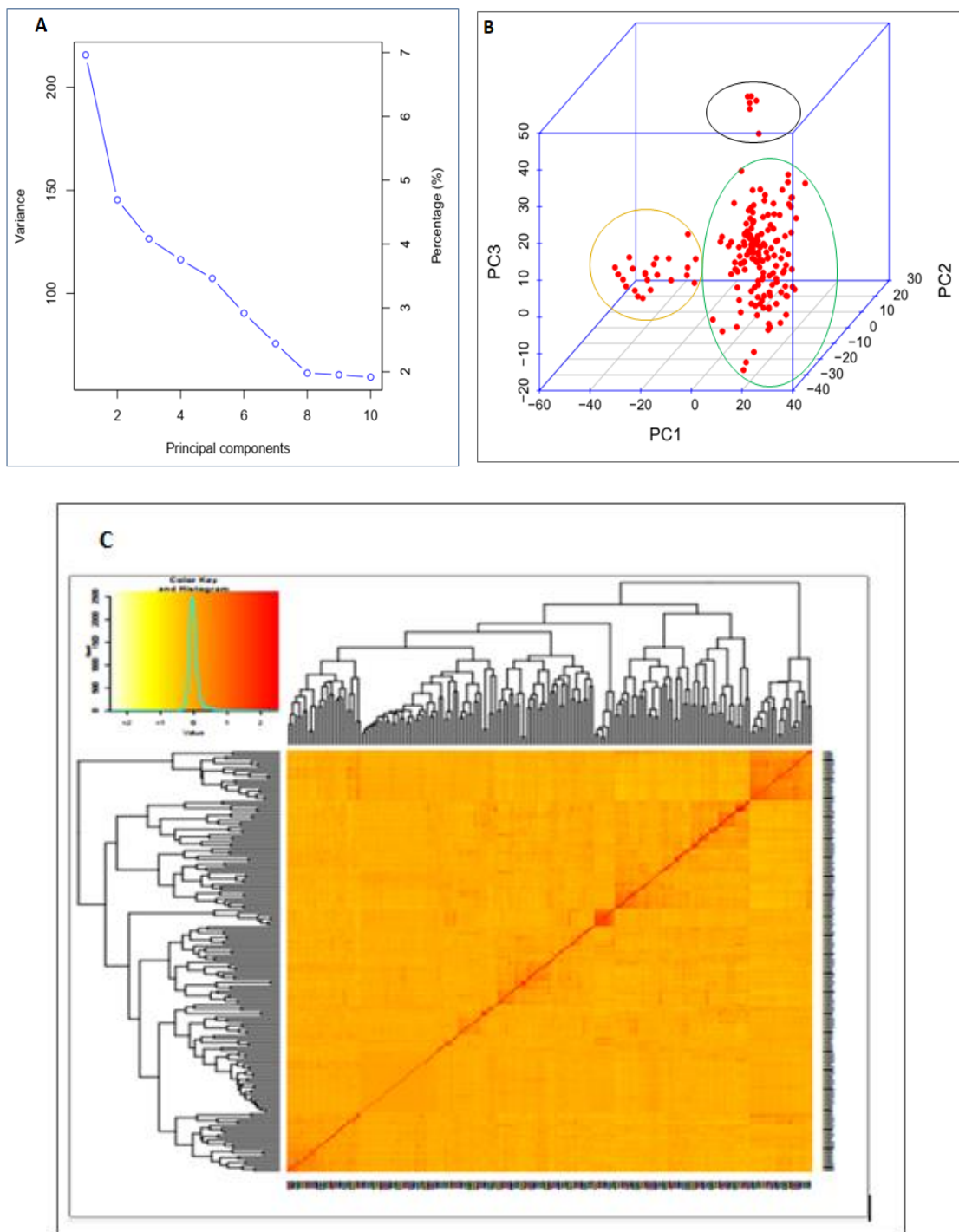


Figure 33. Principal component and familiar relatedness analysis of 178 wheat genotypes using 6,788 SNP markers (A) Scatter plot and (B) 3D plots of the principal components. C) Kinship displayed through a heat map and a tree out of the heat map. The kinship values showed a normal distribution (turquoise curve), and orange represents a weak correlation between pairs of individuals in the panel while red shows a high correlation. The resulting clustering tree is indicated outside of the matrix

4.4.1.5 Linkage disequilibrium analysis

For the 6,788 SNP markers across 178 genotypes, LD was calculated. LDs' alleles differ between chromosomes and within sub-genomes (Table 34). The scatter plot of the genome-wide pairwise LD decay plot is shown in Figure 34. Overall, 97,723 (27.61%) of the 338,125 marker pairings with average LD values of $r^2 = 0.11$ showed significant $p \leq 0.01$ LD. The B sub-genome had the highest number of (143,600, or 42.47%) marker pairs, while the D sub-genome had the lowest (75,300, or 22.27%) marker pairs. Comparatively, SNPs on the B sub-genome showed the greatest LD with a mean value of $r^2 = 0.12$. The LD between SNPs declined across all chromosomes at the LD cut-off $r^2 = 0.2$ within a physical distance of 31.44 Mbp (Figure 35). The marker pairs on chromosome 4D and 2D showed the poorest ($r^2 = 0.03$, and strongest $r^2 = 0.21$) (Table 34).

Table 34. Summary of LD analysis among marker pairs per chromosome and sub-genomes

Chr	Total marker pairs	r ²	Distance (Mbp)	Significant marker pairs (P<0.01)	Chr	Total marker pairs	r ²	Distance (Mbp)	Significant marker pairs (P<0.01)
1A	12,475	0.11	58.05	5,032 (35.06)	5B	22,750	0.14	40.22	8,193 (36.01)
1B	19,900	0.10	44.93	5,820 (29.8)	5D	11,100	0.12	59.51	2,273 (20.48)
1D	10,250	0.13	72.36	1,783 (17.40)	6A	14,700	0.08	57.51	3,928 (26.72)
2A	21,200	0.15	50.03	7,342 (34.63)	6B	18,800	0.11	50.53	6,163 (32.78)
2B	28,100	0.11	36.88	9,511 (33.85)	6D	7,950	0.05	87.75	911 (11.46)
2D	14,550	0.21	57.45	4,771 (32.79)	7A	22,750	0.09	42.53	6,382 (28.05)
3A	17,450	0.09	57.38	4,259 (24.41)	7B	22,450	0.11	42.47	7,492 (33.37)
3B	22,000	0.12	49.85	6,795 (30.89)	7D	14,100	0.08	60.62	2,246 (15.93)
3D	14,650	0.12	56.41	3,940 (26.90)	A Sub-genome	119,225	0.11	56.04	35,012 (29.44)
4A	13,050	0.11	75.78	3,830 (29.35)	B sub-genome	143,600	0.12	51.63	47,527 (33.24)
4B	9,600	0.14	96.54	3,463 (36.08)	D sub-genome	75,300	0.11	65.7	15,184 (20.16)
4D	2,700	0.03	218.8	1,71 (6.34)	Total	338,125	0.11	57.79	97,723 (27.61)
5A	17,600	0.09	52.97	4,897 (27.83)					

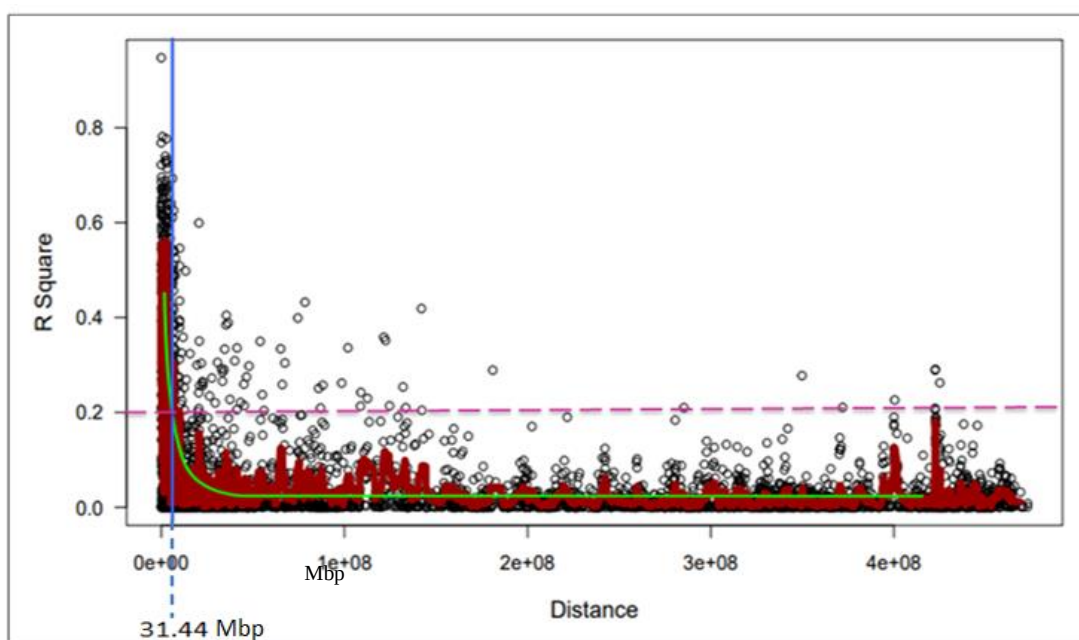


Figure 34. Genome-wide LD decay plot over physical distance based on 6,788 SNP markers. The green curve represents the model fits to LD decay. The horizontal magenta dash-line represents the arbitrary threshold for no LD ($r^2 = 0.2$). The vertical blue line indicates the intersection between the critical r^2 value and the average map distance (31.44 bp) to determine QTL confidence intervals.

4.4.1.6 Genome-wide association study

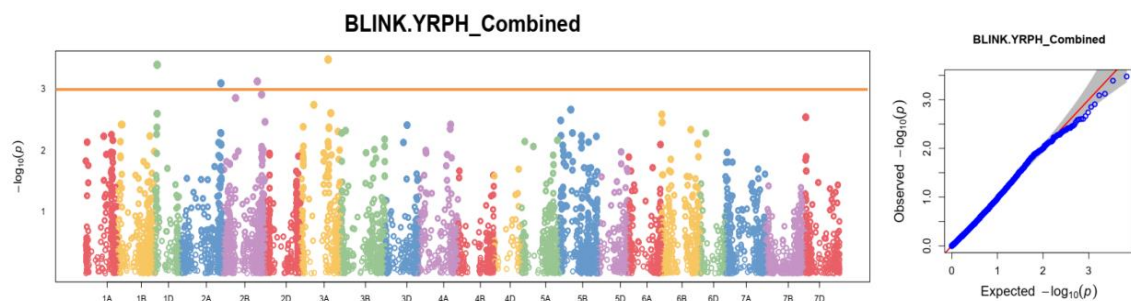
Linkage-disequilibrium and Bayesian information were used in the MTA analysis. At a nominal *p-value* of 0.001, or $-\log_{10}(0.001) = 3$ the BLINK statistical model-based association analysis discovered 148 SNPs significantly associated with the coefficient of infection. Supplementary Table 5 shows MTAs that exceeded the nominal *p-value* of 0.001 or $-\log_{10}(0.001) = 3$ significance thresholds for yellow rust resistance at pre-heading, heading, flowering, mid-maturity, and maturity growth stages. In addition, allele identity, marker position, *p-values*, additive effects, and r^2 of the identified MTAs were computed. Among 148 identified MTAs, 17 (11.49%) MTAs conferred yellow rust resistance at pre-heading, 24 (16.22%) at heading, 34 (22.97%) at flowering, 21 (14.19%) at mid-maturity, 25 (16.89%) at the level of maturity, and 27 (18.24%) MTAs for all stages were effective. The percentage of phenotypic variation explained by the markers varied significantly from 1.3% for yellow rust resistance measured at heading at Holeta to 14.14% for the resistance measured in the pre-heading stage at Meraro.

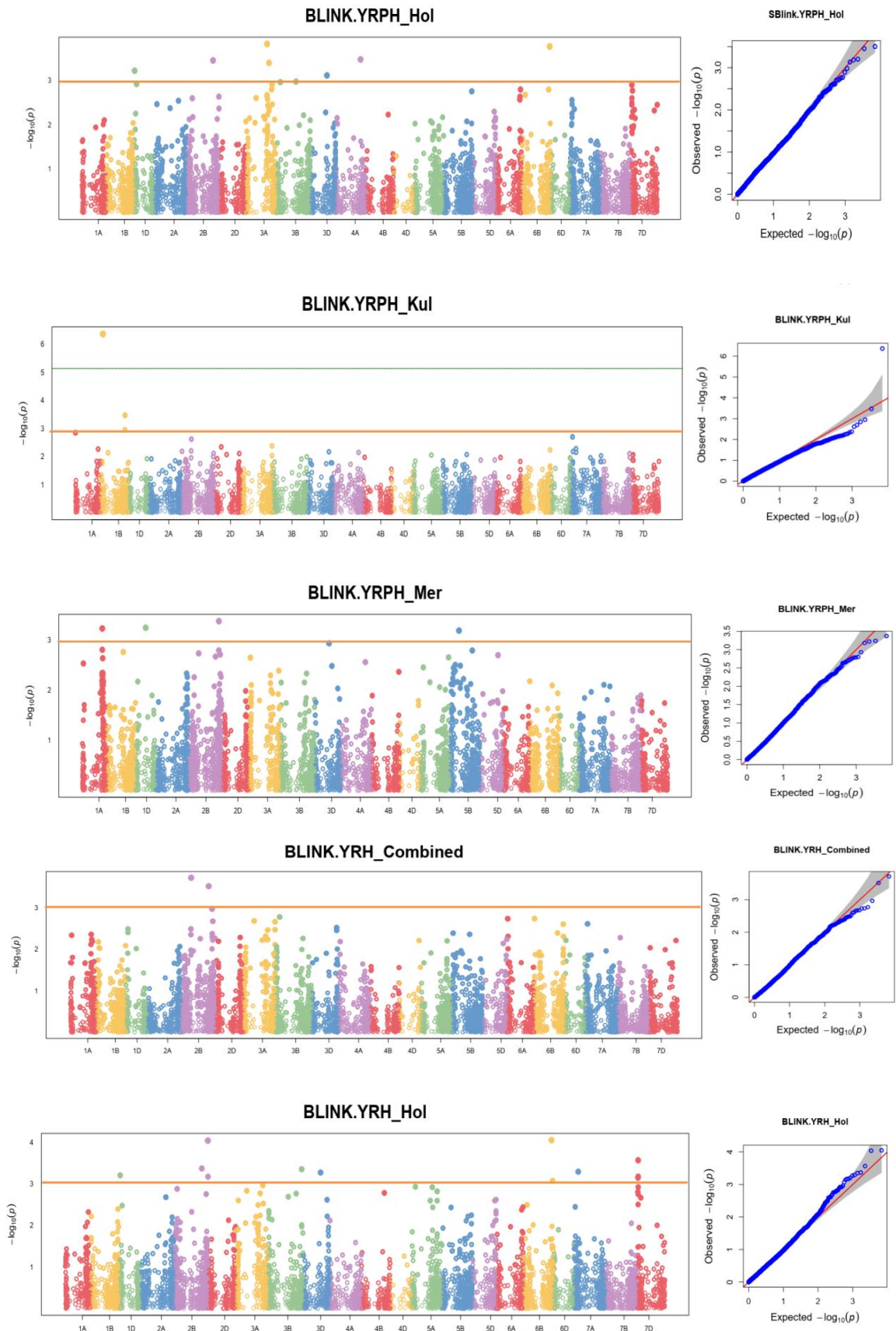
At the pre-heading stage, the proportion of phenotypic variation (r^2) explained by the detected significant markers extended from 2.19% for the SNP 1214020|F|0-68:A>C-

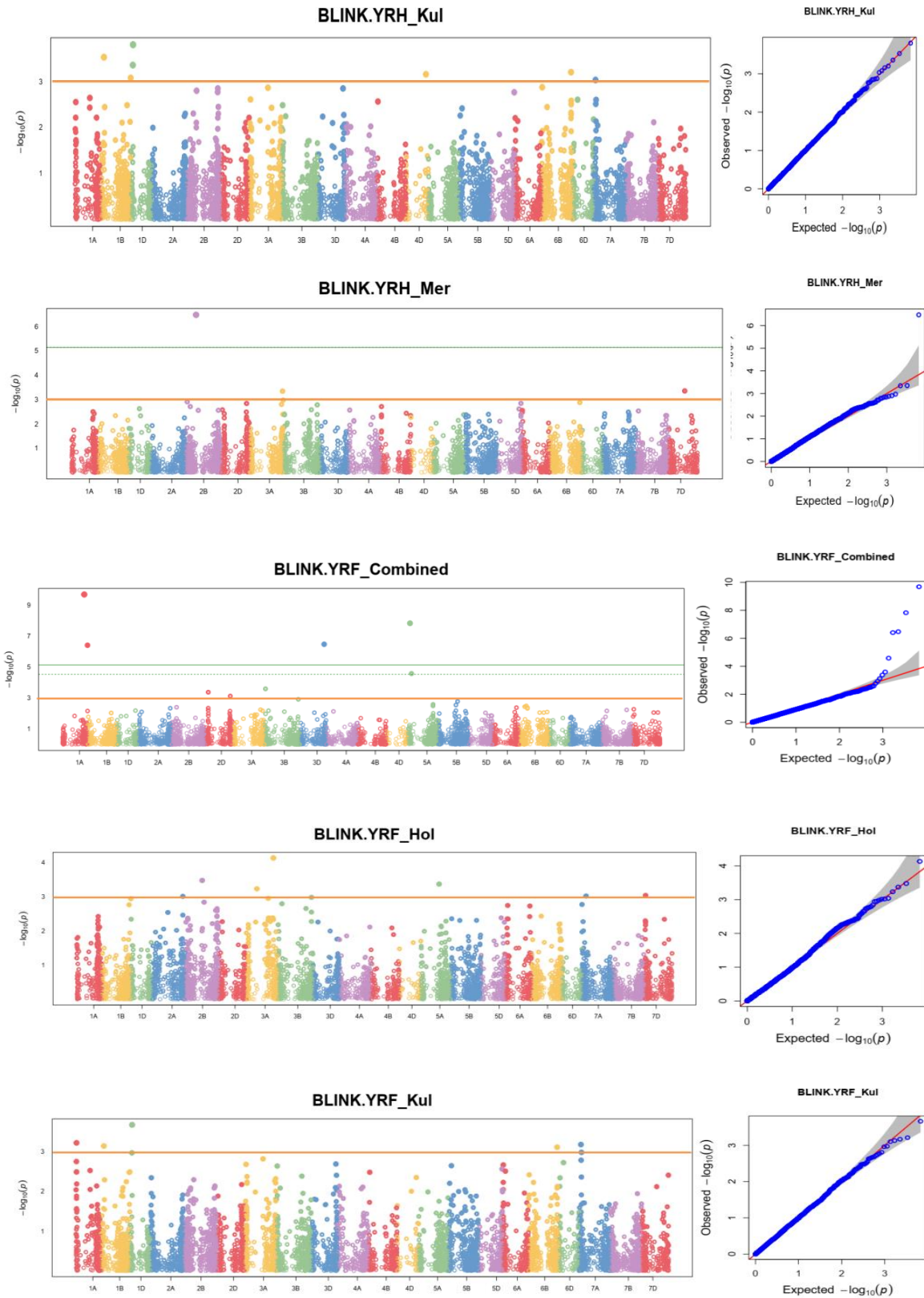
68:A>C on chromosomes 1D to 14.14% for the SNP 5969589|F|0-49:C>G-49:C>G on 1D. Likewise, the proportion of phenotypic variation (r^2) explained by the significant SNP markers at the heading stage ranged from 1.3% for 3020463|F|0-7:A>G-7:A>G and 1000215|F|0-22:G>T-22:G>T A on chromosomes 1A to 11.09% for 4910323|F|0-27:C>A-27:C>A on 1D. Similarly, the r^2 for MTAs for yellow rust resistance at flowering ranged from 9.74 - 14.05% for the allele 1062638|F|0-63:G>A-63:G>A and 1000215|F|0-22:G>T-22:G>T A on chromosomes 1A and 2A, respectively. The r^2 of MTAs for yellow rust resistance at mid-maturity ranged from 8.71 - 13.63%, for the SNP markers 1115117|F|0-21:T>C-21:T>C and 1094246|F|0-48:A>G-48:A>G on chromosomes 1A and 2B respectively. Moreover, the phenotypic variance explained by the MTAs at maturity for yellow rust resistance ranged from 7.1% for the SNP 1245237|F|0-24:G>A-24:G>A on chromosomes 2A to 14.05% for the SNP marker 2264044|F|0-68:T>C-68:T>C on chromosomes 3B. Furthermore, the proportion of yellow rust resistance explained by the significant alleles at the maturity stage ranged from 7.94% for the allele whereas the allele 4008773|F|0-17:G>A-17:G>A on chromosomes 2B to 13.63% for the SNP 1094246|F|0-48:A>G-48:A>G on chromosomes (Supplementary Table 5).

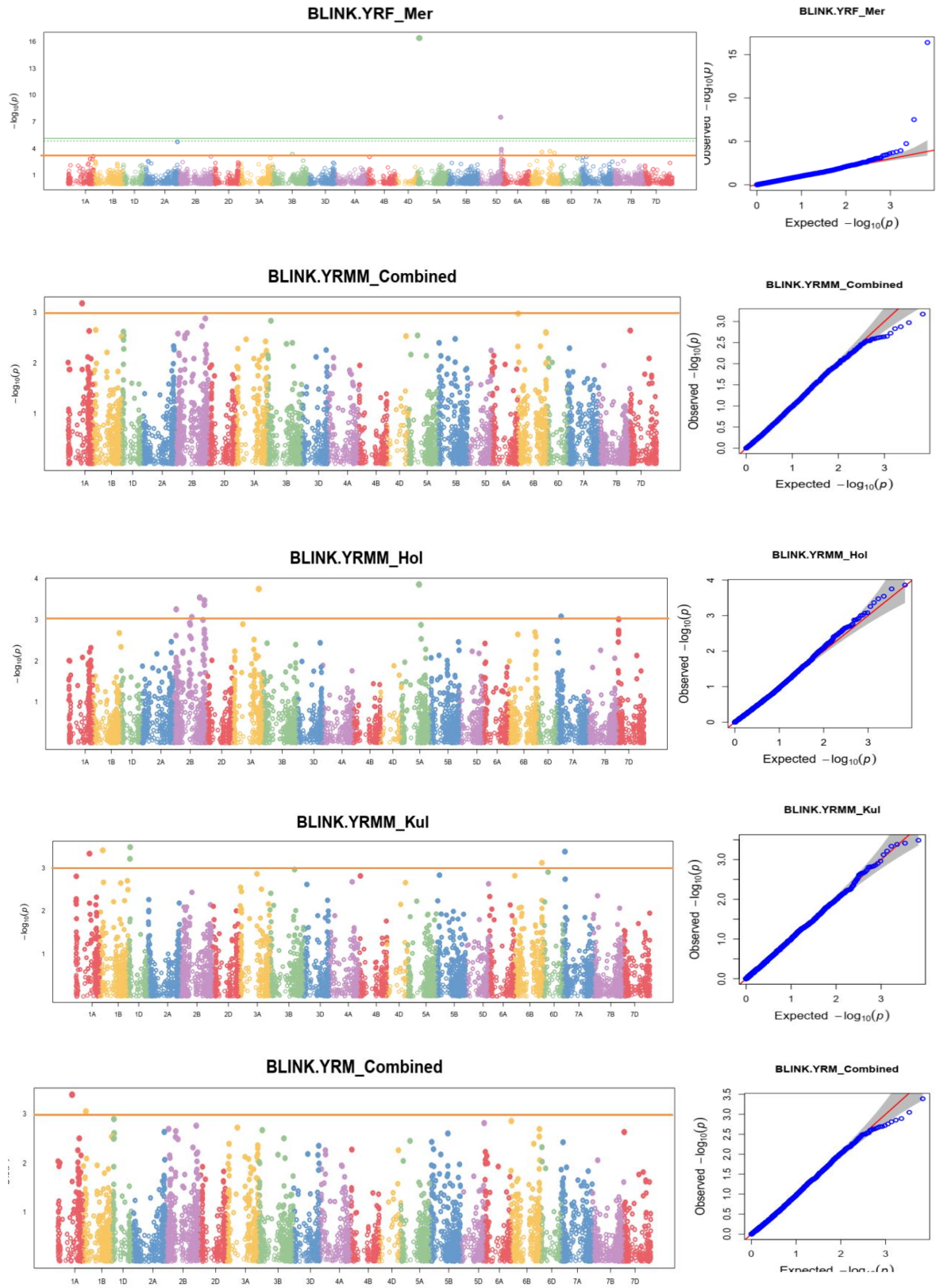
A genome-wide scan for the coefficient of infection in individual environments identified significant markers associated with yellow rust resistance at different locations. For instance, MTA analysis at Holeta identified six MTAs significantly associated with yellow rust resistance at the pre-heading stage on chromosomes 1D, 2B, 3A, 5A, 3D, 4A, and 6B; 12 MTAs at the heading stage on chromosomes 1D, 2B, 3B, 6B, 7A, and 7D; seven significant MTAs conferring coefficient of infection at the flowering stage on chromosomes 2A, 2B, 3A, 5A, 7A, and 7D; nine MTAs at the mid-maturity stage on chromosomes 2B, 3A, 5A, 7A, and 7D; eight significant MTAs at the maturity stage on chromosomes 2B, 3A, and 6A; and seven MTAs for yellow rust resistance across all stages on chromosomes 2B, 3A, 5A, 7A, and 7D. The analysis revealed that MTAs on chromosome 2B conferred stable yellow rust resistance across all growth stages at Holeta. Likewise, a GWA scan for yellow rust resistance at Kulumsa identified 30 MTAs conferring resistance to the coefficient of infection at various growth stages: two MTAs at the pre-heading stage on chromosome 1B; seven MTAs at the heading stage on chromosomes 1D, 4D, 6B, and 7A; four MTAs at the flowering stage on chromosomes 1A, 1B, 1D and 7A; six MTAs at the mid-maturity

stage on chromosomes 1A, 1B, 1D, 6B and 7A; five MTAs at the maturity stage on chromosomes 1D, 1B and 7A; and six MTAs for yellow rust resistance across all stages on chromosomes 1A, 1B, 1D, 6B and 7A. Moreover, a GWA scan for the yellow rust resistance analysis at Meraro discovered numerous (46) MTAs that confer resistance to yellow rust at various growth stages. The analysis identified four MTAs at the pre-heading stage on chromosomes 1A, 1D, 2B, and 5B; three MTAs at the heading stage on chromosomes 2B, 3A, and 7D; 15 MTAs at the flowering stage on chromosomes 1A, 2A, 2B, 3B, 4B, 5A, 5D, 6B, and 7A; five MTAs at the mid-maturity stage on chromosomes 2B, 3A, 4B and 6B; eight MTAs at the maturity stage on chromosomes 2D, 3A, 4A, 4B, 5A, 6B and 7A; and 11 MTAs for yellow rust resistance at all stages of growth on chromosomes 1A, 1B, 2D, 3A, 3B, 3D, 4B, and 5A. The combined measure of yellow rust resistance across locations at the heading, mid-maturity, and maturity stages provided significant associations. It found 20 MTAs, including one at mid-maturity on chromosomes 1A, two at the maturity stage on chromosomes 1A and 1B, and two for yellow rust resistance across locations and all stages on chromosomes 3A and 3B (Supplementary Table 5, Figure 35). Eight MTAs were found at the flowering stage on chromosomes 1A, 2D, 3D, 5A, and 7A; one MTA at the mid-maturity stage on chromosomes 1A; two MTAs at the maturity stage on chromosomes 1A and 1B; and two MTAs for yellow rust resistance across locations and all stages on chromosomes 3A and 3B. It was observed that MTAs on chromosome 7A were detected to contribute to stable yellow rust resistance across all environments. The allele contributes to yellow rust resistance at the flowering stage across all environments. Moreover, the allele on chromosome 2B was found to confer yellow rust resistance at Holeta and Meraro.









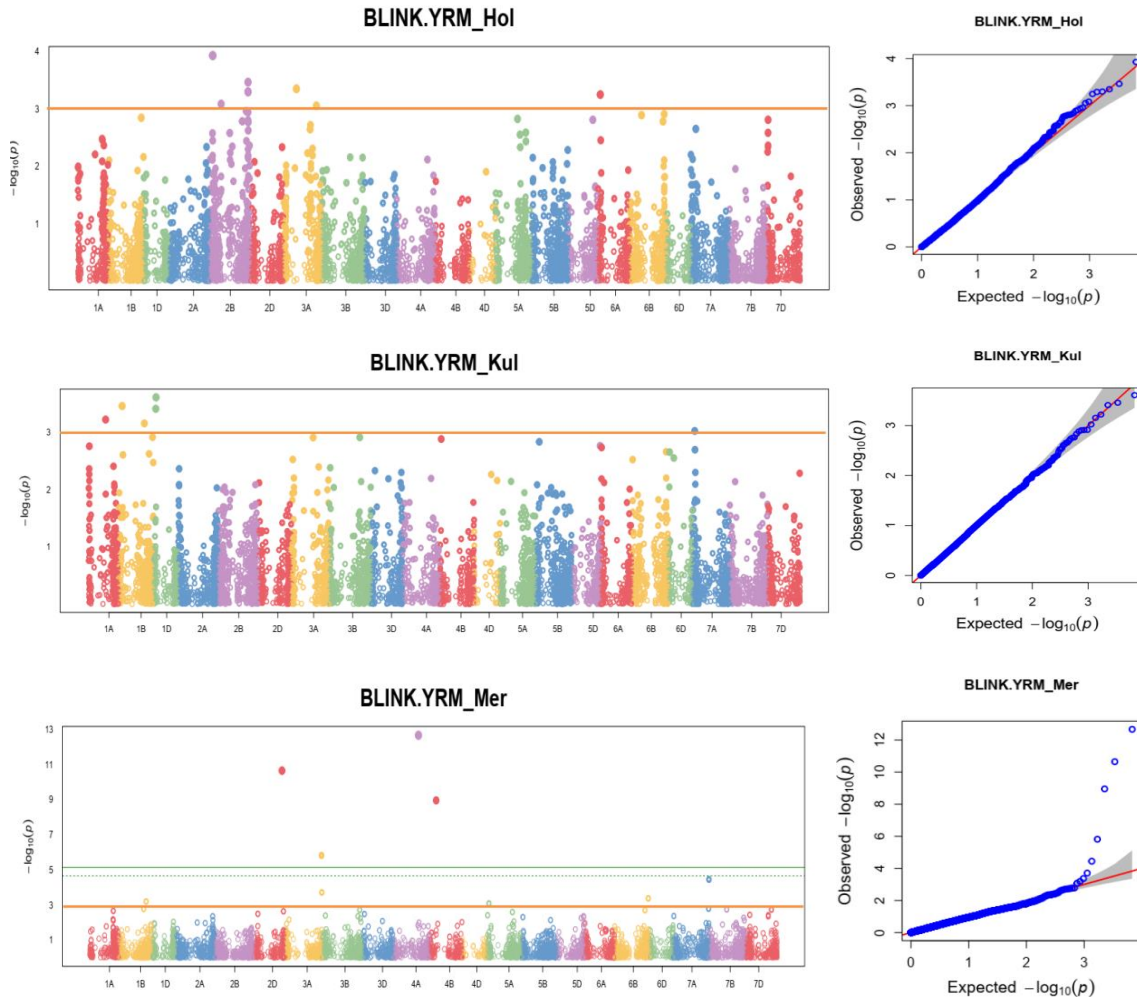
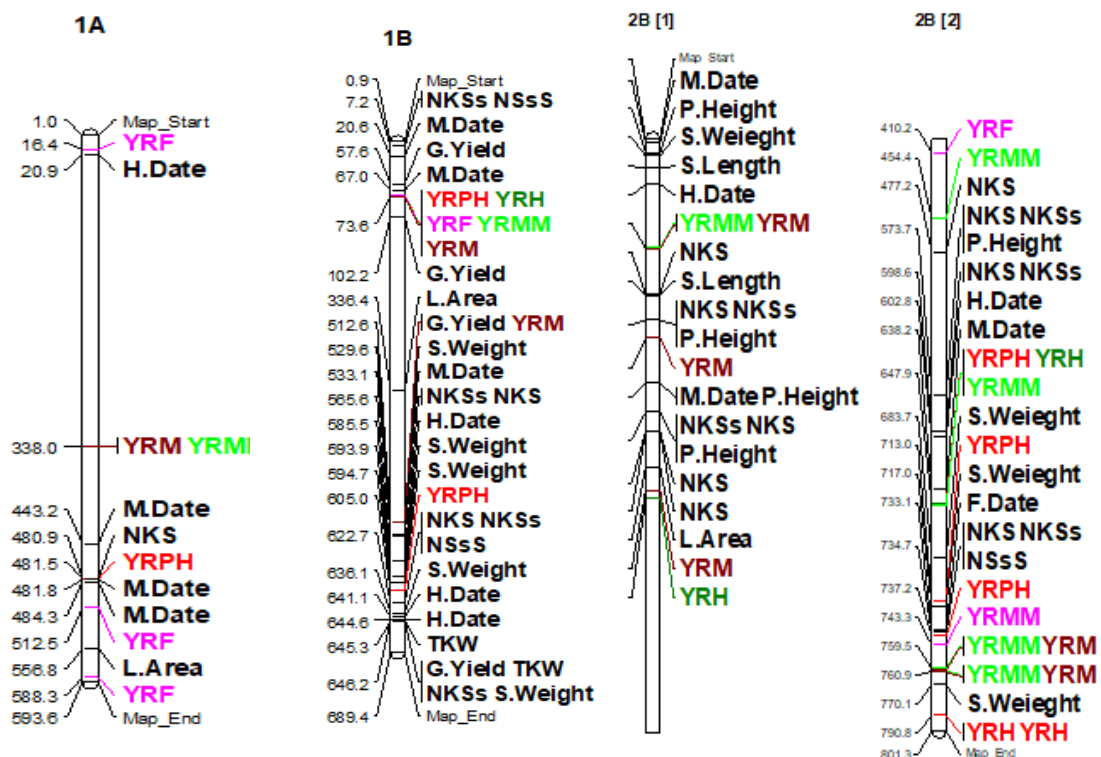
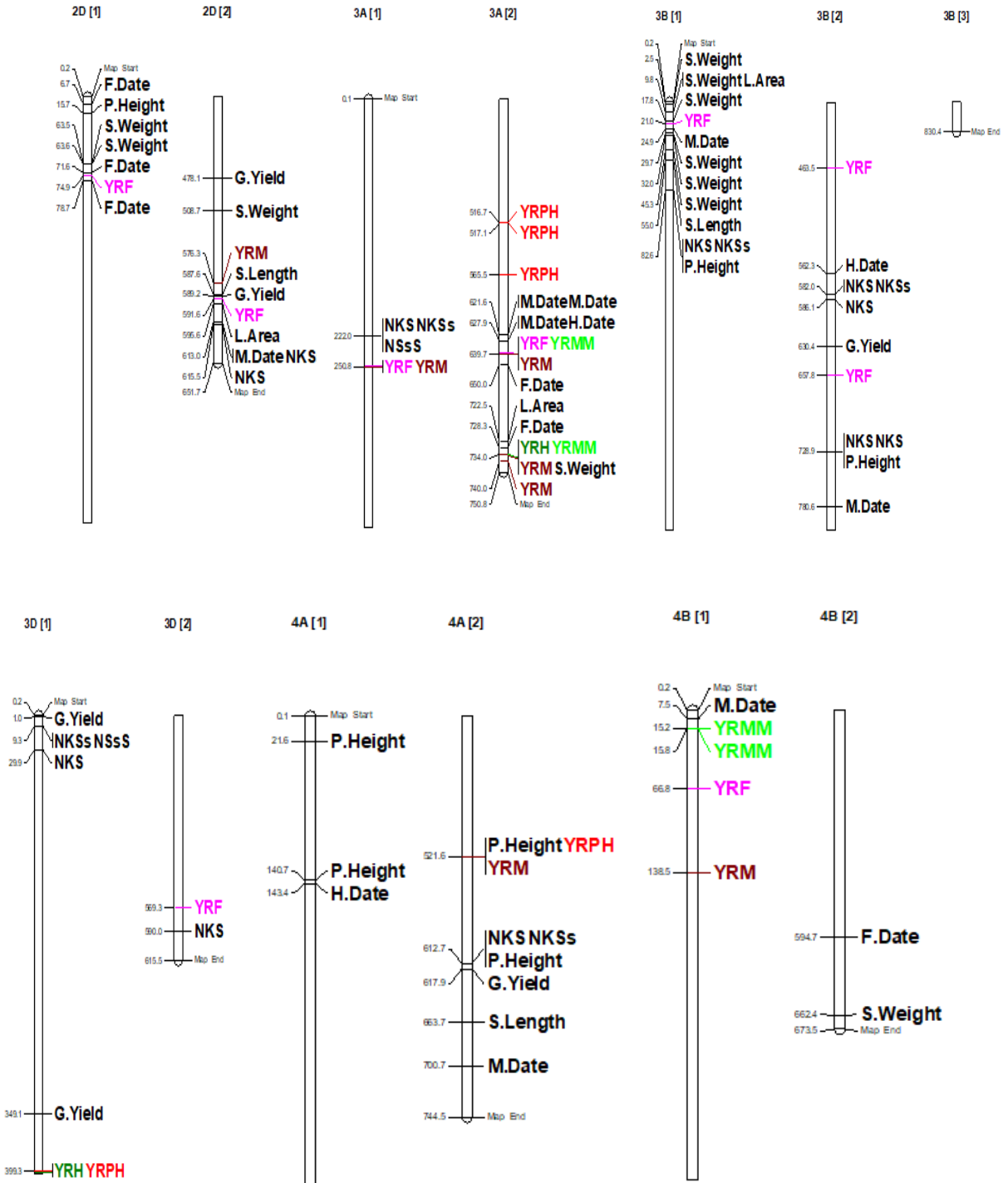


Figure 35. Some examples of Manhattan plots for the coefficient of infection and GWAS scans resulting in significant associations, each dot represents an SNP. On the x-axis is the genomic position of the SNPs on the corresponding chromosomes indicated in different colors. On the y-axis is the $-\log_{10}$ of the p -value depicting the significance of the association test. The horizontal orange line is the nominal p -value 0.001 significance threshold used in the association analysis for YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, and YRM = coefficient of infection at maturity. The quantile-quantile (Q-Q) plots at the right side of the Manhattan plots indicate how well the used BLINK model accounted for population structure and kinship for each of the disease traits. In each plot, the observed $-\log(P \text{ values})$ from the fitted GWAS models (y-axis) are compared with their expected value (x-axis) under the null hypothesis of no association with the trait. Each blue dot represents a single nucleotide polymorphism; the red line is the model for no association.

The coefficient of infection putative QTLs were discovered by combining the MTAs based on their physical distance in Mbp. MTAs on the same linkage group within the physical distance for LD decay specific to that chromosome were assigned to the same putative QTL (Supplementary Table 6, Figure 36). Accordingly, the 148 MTA markers were assigned to 54 putative coefficients of infection QTLs based on our LD criteria.

The association analysis for yellow rust resistance at pre-heading in individual environments found 12 putative QTLs that were on chromosomes 1A (qYrS.02), 1B (qYrS.06 and qYrS.08), 1D (qYrS.09, qYrS.10, and qYrS.11), 2A (qYrS.12), 2B (qYrS.17 and qYrS.18). It was observed that some of the detected putative QTLs were effective for the coefficient of infection at several growth stages while others contributed to the coefficient of infection at a particular growth stage (eg. qYrS.56 contributed to yellow rust resistance at the maturity stage). For instance, qYrS.10 contributed to a stable coefficient of infection at the pre-heading, heading, mid-maturity, and maturity stages. Similarly, qYrS.28 was found to be effective for yellow rust resistance at the heading, flowering, mid-maturity, and maturity stages. qYrS.02 also contributed to the coefficient of infection at the pre-heading, mid-maturity, and maturity stages. qYrS.54 was effective for yellow rust resistance at the heading, flowering, and maturity stages. Likewise, qYrS.13 contributed to resistance in later stages such as the mid-maturity, and maturity stages. Putative QTLs that contributed to stable yellow rust resistance from the flowering to maturity stages include qYrS.20, qYrS.27, qYrS.28, and qYrS.43. Supplementary Table 6 presents more information on the detected putative QTLs.





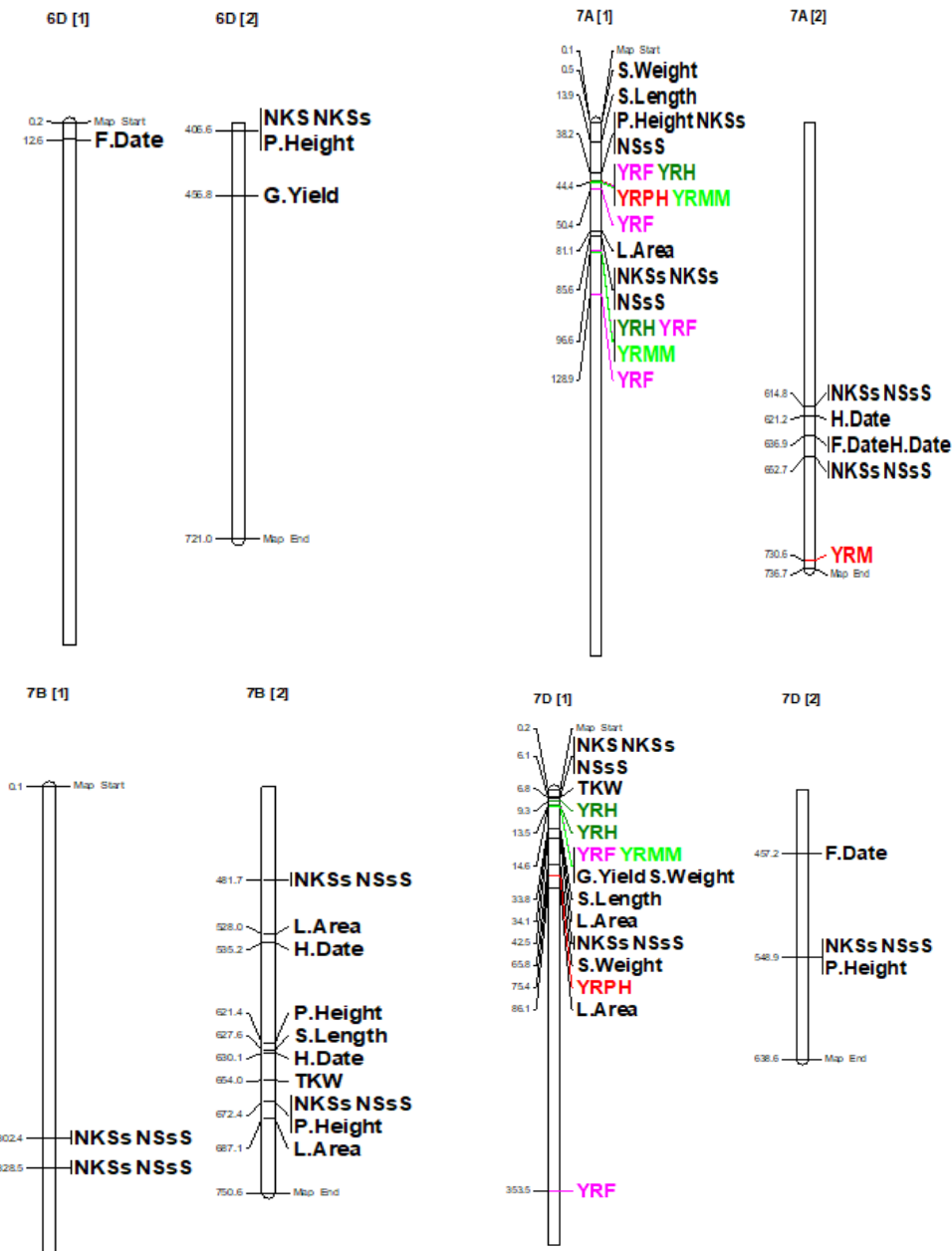


Figure 36. Genomic positions of detected putative QTLs effective for the coefficient of infection. Significant DArTSeq SNPs are presented according to their physical positions on chromosomes in million base pairs. The putative QTLs identified in this study for the MTAs are indicated on the right side of the bars. YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSs= number of spikelets per spike, NKS= number of kernels per spike, NKs= number of kernels per spikelets, SW= spike weight, and GYPP=grain yield per plot.

By annotating genes detected in the QTL regions using the recently released IWGSC RefSeq Annotation v2.1, the functional relationship between the identified QTLs and yellow rust resistance were further studied. Annotation identified several resistance-associated genes that are involved in the plant defense system (Supplementary Table 6). Some of the identified high-confidence candidate genes involved in defense response to fungus include *TraesCS1A02G325400* on chromosome 1A, *TraesCS1B02G067000* on 1B, *TraesCS1D02G018500* on 1D, *TraesCS2B02G548900* on 2B, *TraesCS2D02G497400* on 2D, *TraesCS3A02G395300*, on 3A, *TraesCS3B02G041900* on 3B, *TraesCS3D02G461200* on 3D, *TraesCS4A02G312500* on 4A, *TraesCS4B02G074400*, on 4B, *TraesCS4D02G286100* on 4D, *TraesCS5D02G483900* on 5D, *TraesCS6A02G083200* on 6A, *TraesCS6B02G328600* on 6B, and *TraesCS7A02G028300* on 7A. Furthermore, regarding high-confidence candidate genes important for systemic acquired resistance (SAR), it has been revealed that wheat has a long-lasting, broad-spectrum resistance to pathogen infections. These include *TraesCS1A02G18340* on 1A, *TraesCS1B02G324300* and *TraesCS1B02G480300* on 1B, *TraesCS1D02G018500* on 1D, *TraesCS2A02G540000* on 2A, *TraesCS2B02G533800*, *TraesCS2B02G535000* and *TraesCS2B02G583600* on 2B, *TraesCS3B02G041900* on 3A, *TraesCS5D02G480600*, *TraesCS5D02G501100* and *TraesCS5D02G501800* on 5D, *TraesCS7A02G026100* and *TraesCS7A02G175200* on 7A, and *TraesCS7D02G016800* on 7D. Focusing on the significant QTL regions identified that high-confidence genes *TraesCS1B02G324300* on 1B, *TraesCS6B02G017900* on 6B, *TraesCS7A02G175200* on 7A and *TraesCS7D02G016800* on 7D regulate mitogen-activated protein kinase (MAPK) cascades, which are involved in signaling a variety of plant defense responses against pathogen infections (Meng and Zhang, 2013) (Supplementary Table 7).

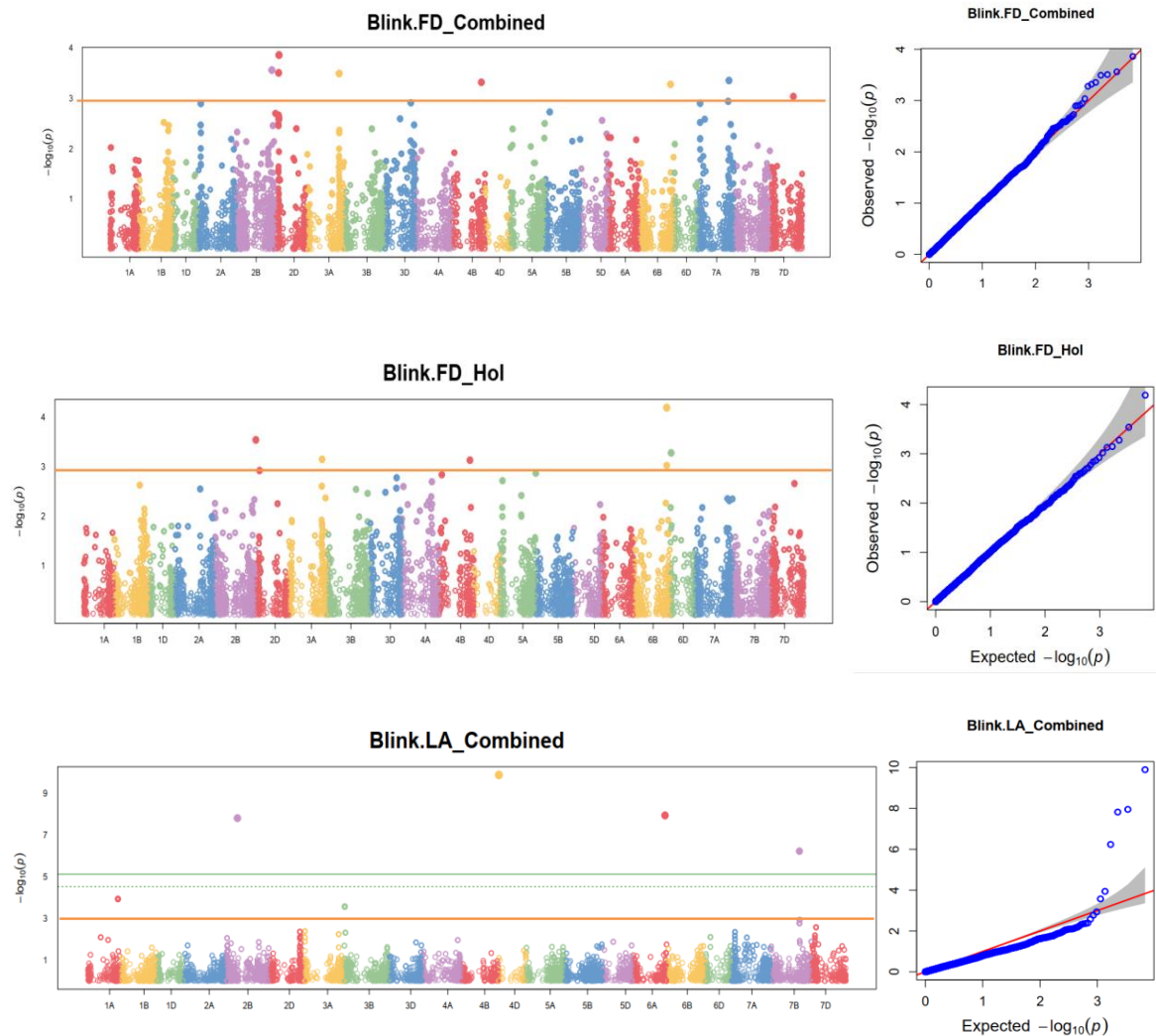
4.4.1.7 MTAs for agronomic traits

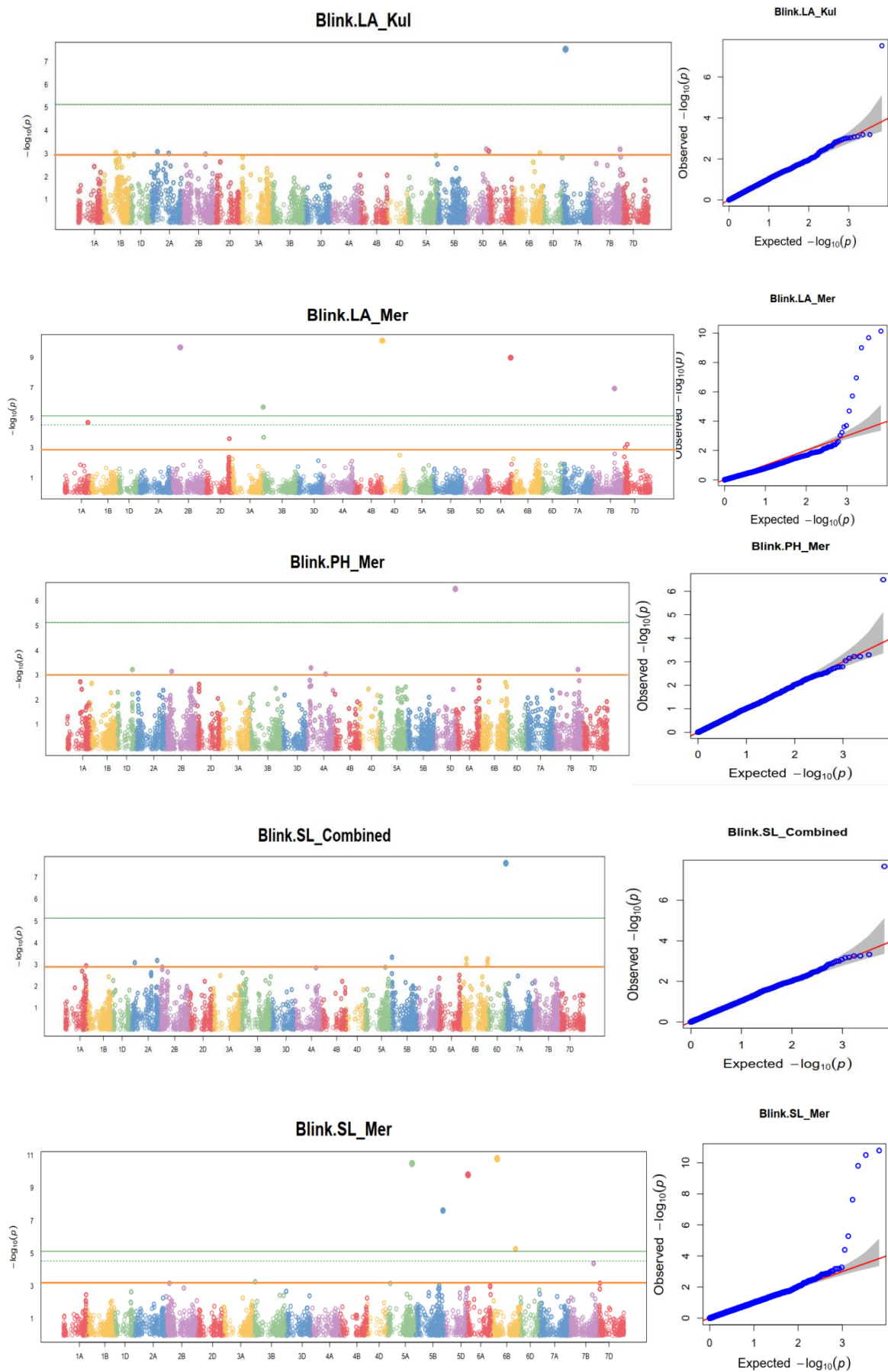
The association analysis for some agronomic traits, including FD, LA, PH, SL, NKS, and SW, resulted in significant MTAs at the nominal *p-value*. For instance, a GWA scan for days to 50% flowering for pooled dates resulted in seven MTAs on chromosomes 2B, 2D, 3A, 4B, 6B, 7A, and 7D. However, dissecting the traits in individual environments detected considerable MTAs at the nominal significance threshold. The same trait provided six MTAs that were produced by days to flowering on chromosomes 2D, 3A, 4B, 5A, 6B, and 6D. The identified SNPs explained 11.66% (1123012|F|0-16:G>C-16:G>C on 6B) to 14.70% (1090345|F|0-8:T>A-8:T>A on 6B) of

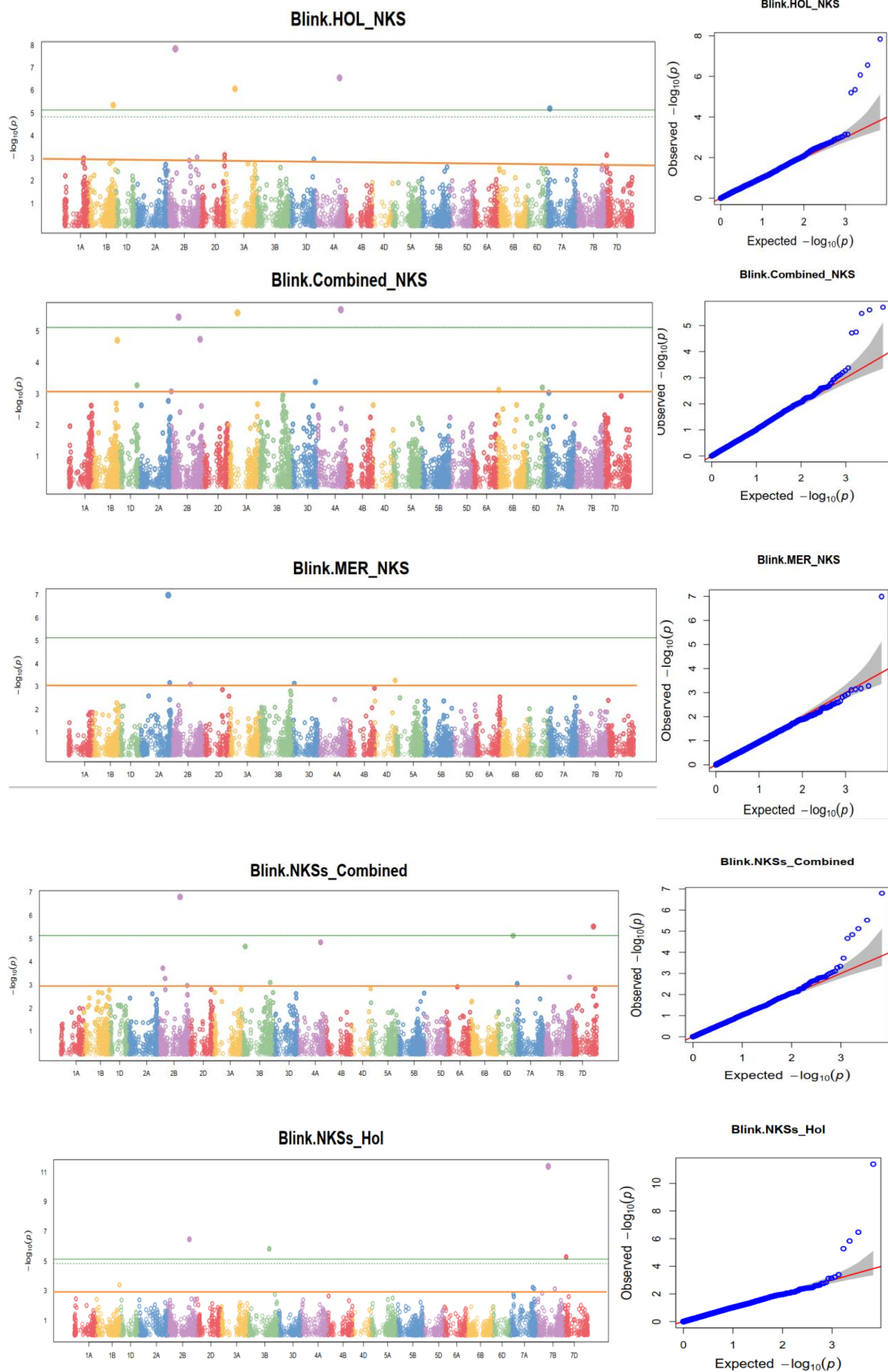
the total variations in days to flowering. Likewise, the association analysis for leaf area identified six MTAs on chromosomes 1A, 2B, 3B, 4D, 6A, and 7B at Holeta; seven MTAs at Kulumsa on chromosomes 1B, 3A, 5D, 6A, 6B, and 7A; and eight MTAs at Meraro on chromosomes 1A, 2B, 2D, 3B, 4D, 6A, 7B, and 7D. The identified SNPs explained 10.04-17.29% of the total variation in leaf area for the SNP markers 1119123|F|0-11:C>G-11:C>G on chromosome 1D and 1265768|F|0-44:T>C-44:T>C on chromosome 4D, respectively. The association analysis for plant height data collected at Meraro identified five MTAs pointing to chromosomes 1D, 2B, 4A, 5D, and 7B. The identified SNPs explained 6.61% (3025953|F|0-25:G>A-25:G>A on 4A) to 12.30% (SNP 1099369|F|0-26:C>T-26:C>Ton 5D) of the total phenotypic variance for plant height (Supplementary Table 8, Figure 36).

The association analysis for pooled spike length identified five MTAs on chromosomes 1A, 2A, 5B, 6B, and 7A. Analysis of the pooled data for days to maturity identified significant SNPs on chromosomes 1B, 2A, 2B, 3A, 5B, and 5D. The association analysis for days to maturity in individual environments identified 9 MTAs at Holeta on chromosomes 1A, 1B, 3B, 5A, and 5B; nine MTAs on chromosomes 1B, 1D, 3A, 3B, 4B, 5B, and 7A for data collected at Kulumsa; and eight MTAs on chromosomes 1B, 2A, 2B, 4A, 5D, 6A and 6B for days of maturity collected at Meraro (Supplementary Table 6). The identified SNPs explained 5.54% to 8.04% of the total variations in days to maturity for the SNPs 1104531|F|0-39:T>A-39:T>A on 2B and 4911245|F|0-46:A>G-46:A>G on 6B, respectively. Association analysis for the pooled number of kernels per spike identified eight MTAs on chromosomes 1B, 1D, 2B, 3A, 3D, 4A, 6B, and 6D. Analyses of the same trait at Meraro provided five MTAs pointing to chromosomes 1D, 2B, 4A, 5D, and 7B. The identified SNPs explained 6.62% of 3025953|F|0-25:G>A-25:G>A on 4A to 13.64% (for 992022|F|0-9:G>A-9:G>A) of the total variations of days to maturity (Supplementary Table 8, Figure 37). GWAS for cumulative number of kernels per spikelets identified seven MTAs pointing to the chromosomes 1B, 3B, 4A, 6D, 7A, 7B, and 7D. The same trait analysis at each individual environment revealed 20 MTAs: six at Holeta on chromosomes 1B, 2B, 3B, 7A, 7B, and 7D; seven at Kulumsa on chromosomes 1B, 2A, 3D, 5A, 5D, 6A, and 7B; and seven at Meraro on chromosomes 1B, 2B, 2D, 3A, 4A, 7A, and 7D. The obtained SNPs explained 6.75-19.15% of the total phenotypic variations in the number of kernels per spikelets by the SNPs 1081747|F|0-27:T>C-27:T>C on 1B respectively.

The association analysis for spike weight found four MTAs on chromosomes 2D, 3A, 3B, and 5B at Kulumsa, and seven MTAs were found on chromosomes 1B, 2B, 2D, 3B, 4D, 5D, and 6A at Meraro. Similarly, the association analysis for kernels per spike at Meraro identified five MTAs pointing to chromosomes 1D, 2B, 4A, 5D, and 7B. The identified SNPs explained 7.50-11.06% of the total variations in kernels per spike for the SNPs 1000905|F|0-46: A>G-46:A>G on 3B and 1126316|F|0-23:A>G-23:A>G on 2B, respectively (Supplementary Table 8, Figure 37). The study showed that certain QTLs discovered for yellow rust resistance overlapped with QTLs for agronomic traits. For instance, the qYrS.12 gene, which was found to be associated with yellow rust resistance at the flowering stage, is co-mapped with the putative QTL found for plant height on chromosome 2A. Similarly, the putative QTL for grain yield discovered on 1B is also co-mapped with the yellow rust resistance identified at the maturity stage (Figure 37).







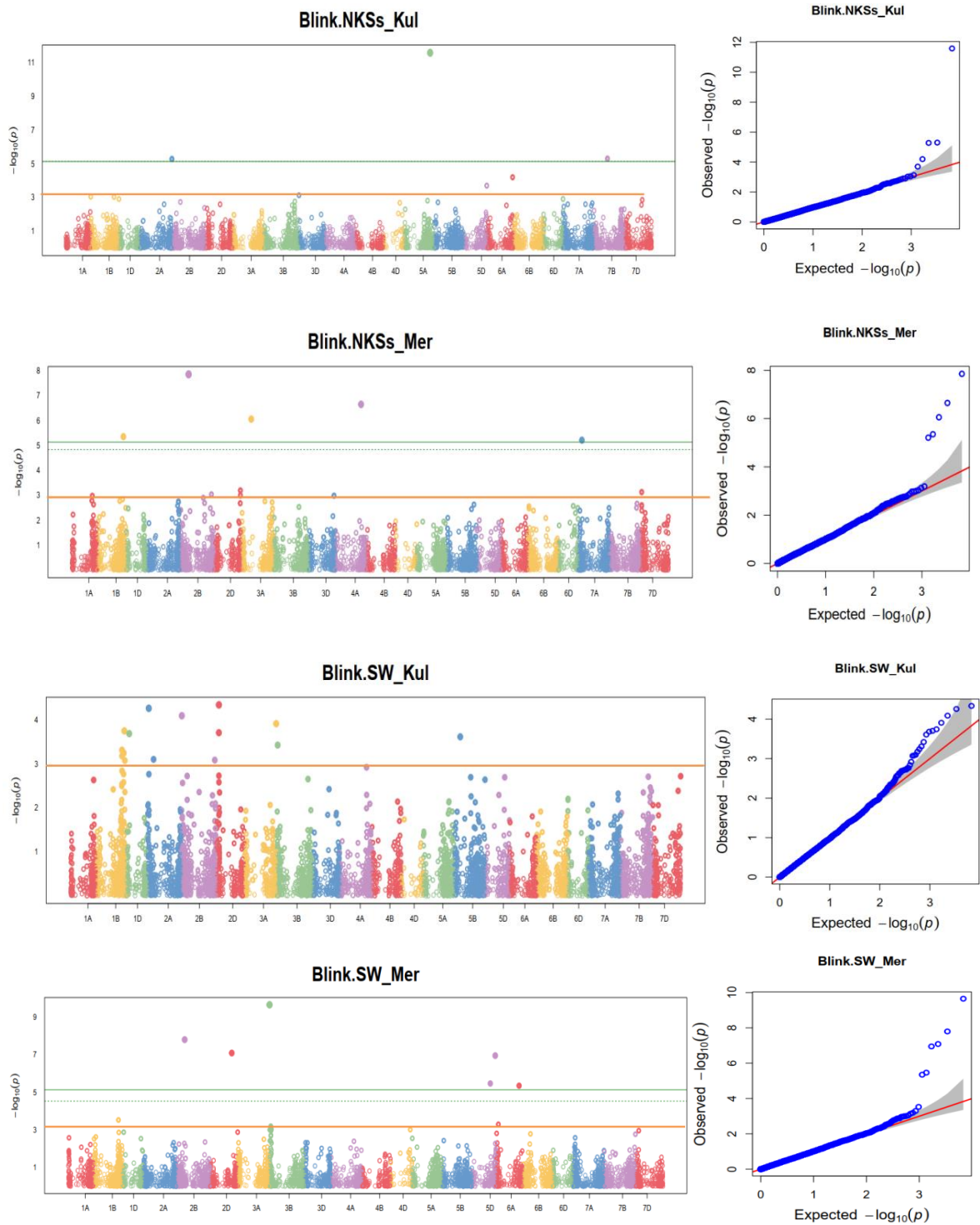


Figure 37. Manhattan plots for agronomic and yield-related traits in each environment and combined data, HD = days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSs= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight, and GYPP=grain yield per plot. The quantile-quantile plots at the right side of the Manhattan plots indicate how well the GWAS model accounted for population structure and kinship for each of the disease traits. In each plot, the observed $-\log(p\text{-values})$ from the fitted GWAS models (y-axis) are compared with their expected value (x-axis) under the null

hypothesis of no association with the trait. Each blue dot represents a single nucleotide polymorphism; the orange line is the model for no association.

4.2.2 Discussion

4.2.2.1 Phenotypic variability in resistance to *Puccinia striiformis* f. sp. *tritici*

The average disease severity and field response of 178 bread wheat genotypes to *P. striiformis* f. sp. *tritici* at Holeta, Kulumsa, and Meraro were recorded in the field. The mean DS, FR, and CI of the tested wheat genotypes at Holeta, Kulumsa, and Meraro were 8.35, 26.92, and 45.08 for DS; 0.22, 0.73, and 8.30 for FR; and 27.55, 45.05, and 47.16 for CI, respectively. Meraro showed the highest DS, FR, and CI, as Meraro is a national hotspot for *P. striiformis* infestation. It is one of the national and international screening sites for the International Center for Maize and Wheat Improvement (CIMMYT) wheat germplasm for yellow rust resistance. The analysis revealed the existence of significant genetic variation among the wheat genotypes examined for a coefficient of infection, suggesting that yellow resistance could be improved through selection breeding. The highest coefficient of infection resistance reaction at maturity stage at Meraro detected in this research (60.24%) is a lower resistance reaction than the reaction response reported by Khalil et al., (2022) (77%) for 426 Indian bread wheat materials. This implies that the Meraro variety exhibits a lower susceptibility to infection compared to the Indian bread wheat materials studied by Khalil et al., (2022). All the considered traits showed moderate heritability ($H^2 = 30 - 60\%$) except for the coefficient of infection at the pre-heading stage which showed low heritability ($H^2 = 27\%$). Narrow-sense heritability, which estimates the proportion of phenotypic variations in yellow rust resistance in a wheat panel, is due to the additive genetic effect and was high ($h^2 = 60\%$), indicating the presence of a strong genetic signal in the data and hence the promising possibility of improving yellow rust resistance by exploiting the resistance source through selection breeding. Comparable high heritability ($h^2 = 88\%$) for yellow rust resistance traits was reported by Zegeye et al., (2014). Similarly, Li et al., (2020) described high heritability ($h^2 = 81\%$) for yellow rust resistance analysis in Chinese endemic wheat genotypes.

Correlation analyses using CI revealed that yellow rust resistance traits were significantly a negative association with leaf area, plant height, thousand kernel weight, number of kernels per spike, spike weight, and grain yield, indicating that high yellow rust infestations have a substantial effect on reducing yield and yield-related traits.

Moreover, plant height has a considerable escaping effect from yellow rust, as the infestation can initiate from the soil. Similarly, a significant negative association between yellow rust infestation and plant height, thousand kernel weight, grain yield, and number of kernels per spike was reported by Solomon (2022) and Saleem et al. (2022). Nevertheless, days to maturity and spike length showed a moderate negative correlation ($r < -0.3$), indicating that late maturing and long spiked genotypes have an escaping mechanism for yellow rust infection. The strong negative associations of yield-related, vegetative, and phenological traits with yellow rust resistance traits indicate that these traits could be considered in indirect selection for yellow rust disease resistance.

4.2.2.2 Population structure, relatedness, and LD

The presence of three sub-populations ($K = 3$) with substantial mixing was supported by analysis of the population structure and principal components. This finding suggests that there is a significant level of gene flow and interbreeding between the populations. Ovenden et al., (2017) showed similar indistinct population grouping, increased admixing, and poor population sub-structuring for 312 wheat genotypes using 5k SNP markers. The existence of cryptic familiar relatedness was also verified by kinship analysis, highlighting the significance of using both population structure (Q) and kinship (K) as covariates in marker-trait association analyses. The population stratification, relatedness, and marker effects have been effectively accounted for using the BLINK model employed in the association studies, reducing the confounding effects that could lead to false-positive MTAs. Visualizing the Q-Q plots helped to confirm effective control of the confounding factors.

According to our study, there is a relatively even distribution of markers among the bread wheat sub-genomes, with the A sub-genome contributing the most (10,317), the B sub-genome coming in second (10,979), and the D sub-genome harboring the least (9,756). Similar findings were published by Vikas, et al., (2022), who found that 6,036 of the 18,932 mapped SNPs were mapped to the A sub-genome, 7,191 to the B sub-genome, and 5,705 to the D sub-genome. This indicates that the history of natural selection, gene conversion, mutation, and other mechanisms that result in gene-frequency evolution is reflected in each genomic region's LD. The A and B sub-genomes had a disproportionately high number of SNPs, which was probably caused by

D sub-genomes had smaller size and the relatively recent joining of the D-genome to the hexaploid wheat genome. The LD varied amongst the three sub-genomes, and it was low for the A and B sub-genomes, perhaps because of their large size and lengthy evolutionary histories in comparison to the D genome.

4.2.2.3 Marker-trait associations and identification of candidate genes

The discovery of significant marker-trait relationships at different growth stages revealed the presence of significant genotypic diversity among the investigated bread wheat genotypes. At a nominally significant threshold of $p\text{-value} \leq 0.001$, GWAS analysis discovered 148 MTAs, pointing to 54 QTLs for the coefficient of infection and 179 MTAs for agronomic traits. Zegeye et al., (2014) also found 38 SNPs in synthetic hexaploid wheat evaluated at Meraro and Arsi Robe. The large sample size and SNPs employed in the current investigation could be the main cause for the considerable variation in the number of significant markers. Among the 18 QTLs reported by Zegeye et al., (2014) for yellow rust resistance, four (1A, 1B, 2B, and 5A) shared the same physical position, which could be due to the difference in the number of used SNPs (2590), genotyping platform (iSelect array), and wheat populations.

In the current study, 48 of the identified yellow rust resistance SNPs were found to be location-specific (at Meraro), showing the presence of *P. striiformis* races at the test site that was distinct from other test sites, along with race-specific resistance genes. The present study confirmed that chromosome 2B contains more yellow rust resistance loci (24 MTAs). Chen et al., (2012) and Mallard et al., (2005), reported approximately 112 *P. striiformis* resistance genes on wheat chromosome 2B, such as: *Yr9*, *Yr10*, *Yr15*, *Yr24/Yr26/YrCh42* (Cheng et al., 2014), *Yr29/Lr46* (Lan et al., 2014), *YrExp1* (McIntosh et al., 2007), and *YrH52* (Klymiuk et al., 2020). Similarly, the present study identified that chromosome 2B harbored many yellow rust resistance putative QTLs, and this finding was in line with the reports of Feng et al., (2018) and Khalil et al., (2022), who described several yellow rust resistance QTLs on the same chromosome, including *Yr64*, *Yr65*, *YrTr1*, *YrAlp*, *YrH122*, *YrL693*, *YrC142*, *YrMY41*, *QYr.cau-1BS*, *QYrco.wpg-1BS.1*, and *QYrco.wpg-1BS.2*. Interestingly, markers found in the current study are located at 74.20-793 Mbp.

Total of 54 QTLs were observed across all environments. Of the 54 QTLs, 17 putative QTLs were detected at Holeta, 3 at Kulumsa, 23 at Meraro, and 11 QTLs were observed in all environments (Table 35). Moreover, 22 of the 54 QTLs were observed across

different growth stages, including 10 QTLs at two different growth stages, seven QTLs in three growth stages, one QTL in four growth stages, and two QTLs in all growth stages (Table 36). The failure to generally not repeat QTL effects across all environments could be due to site-specific QTL effects and different disease pressures. The prolonged and intense rains that characterize Meraro lead to the largest natural yellow rust infestations across all growth stages. Climate factors, including lingering crop moisture and protracted periods of heavy rain, encourage disease infection and dissemination across the crop canopy.

Table 35. Stable putative QTLs across all locations identified through bread wheat chromosomes for the coefficient of infection

No	QTL	Chr	Position (bp)	Phenotypes _Location
1	qYrS.01	1A	16417326	YRF_Combined YRM_Combined, YRM_Kulumsa, YRMM_Combined, YRMM_Kulumsa,
2	qYrS.02	1A	337947849	YRPH_Meraro
3	qYrS.03	1A	512496605	YRF_Combined,
4	qYrS.04	1A	588261371	YRF_Combined, YRF_Meraro YRM_Combined, YRM_Kulumsa, YRMM_Holeta, YRMM_Kulumsa & YRPH_Meraro
5	qYrS.06	1B	73576935	YRH_Holeta & YRPH_Holeta
6	qYrS.09	1D	7734813	YRH_Kulumsa, YRM_Kulumsa , YRMM_Kulumsa, YRF_Kulumsa, YRH_Kulumsa & YRPH_Combined
7	qYrS.10	1D	49605264- 54911805 733216778-	YRF_Holeta & YRPH_Combined
8	qYrS.12	2A	750201766 237588008-	YRM_Holeta, YRH_Combined & YRH_Meraro YRH_Combined, YRH_Holeta, YRMM_Holeta, YRPH_Combined & YRPH_Holeta
9	qYrS.14	2B	243083729	YRF_Combined- YRF_Combined YRF_Holeta, YRGM_Combined, & YRM_Holeta
10	qYrS.17	2B	647897009	YRF_Combined
11	qYrS.22	2D	74936166	YRF_Combined
12	qYrS.24	2D	591603469	YRF_Combined
13	qYrS.25	3A	250818410	YRF_Combined
14	qYrS.29	3B	20999249	YRF_Combined
15	qYrS.35	3D	569281482	YRF_Combined
16	qYrS.36	4A	521603853	YRM_Meraro
17	qYrS.37	4A	603746204	YRPH_Holeta
18	qYrS.38	4B	15149905	YRMM_Meraro & YRMM_Meraro YRM_Meraro, YRF_Combined, YRF_Meraro, & YRF_Combined YRH_Kulumsa, YRMM_Kulumsa,
19	qYrS.42	5A	36021495	YRM_Meraro, YRH_Holeta & YRPH_Holeta YRF_Holeta, , YRH_Holeta, YRMM_Holeta & YRF_Meraro
20	qYrS.53	6B	675702168 96563306-	
21	qYrS.55	7A	128909455	

QTL= Quantitative trait locus; Chr = Chromosomes, Phenotype_Location = coefficient of infection measured at individual or across locations (Holetta, Kulumsa, and Meraro), YRPH =

coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity and YRM = coefficient of infection at maturity

Table 36. Stable putative QTLs across a growth stages identified through bread wheat chromosomes for yellow rust resistance

No	QTLs	Chr	Position	Growth stage	Phenotypes Location
1	qYrS.02	1A	337947849	3	YRM_Combined, YRM_Kulumsa, YRMM_Combined, YRMM_Kulumsa, YRPH_Meraro
2	qYrS.06	1B	73576935	3	YRM_Combined, YRM_Kulumsa, YRMM_Holeta, YRMM_Kulumsa & YRPH_Meraro
3	qYrS.08	1B	687536131	2	YRPH_Kulumsa & YRH_Kulumsa
4	qYrS.09	1D	7734813	2	YRH_Holeta & YRPH_Holeta
5 *	qYrS.10	1D	49605264-54911805	5	YRH_Kulumsa, YRM_Kulumsa, YRMM_Kulumsa, YRF_Kulumsa, YRH_Kulumsa & YRPH_Combined
6	qYrS.12	2A	750201766	2	YRF_Holeta & YRPH_Combined
7	qYrS.13	2B	74203726	2	YRM_Holeta & YRMM_Holeta
8	qYrS.14	2B	237588008-243083729	2	YRM_Holeta, YRH_Combined & YRH_Meraro
9	qYrS.17	2B	647897009	3	YRH_Combined, YRH_Holeta, YRMM_Holeta, YRPH_Combined & YRPH_Holeta
10	qYrS.20	2B	759523837-768053989	3	YRM_Holeta, YRMM_Holeta, YRM_Kulumsa, YRM_Holeta, YRMM_Holeta & YRF_Meraro
11	qYrS.25	3A	250818410	2	YRF_Holeta & YRM_Holeta
12	qYrS.27	3A	639713075	3	YRF_Holeta, YRM_Holeta & YRMM_Holeta
13	qYrS.28	3A	733636208-739951852	3	YRH_Meraro, YRM_Meraro, YRMM_Meraro & YRM_Meraro
14	qYrS.34	3D	339476105	2	YRH_Kulumsa & YRPH_Holeta
15	qYrS.42	5A	36021495	2	YRM_Meraro, YRF_Combined, YRF_Meraro, & YRF_Combined
16	qYrS.43	5A	429474426	2	YRF_Holeta, & YRMM_Holeta
17 *	qYrS.53	6B	675702168	5	YRH_Kulumsa, YRMM_Kulumsa, YRM_Meraro, YRF_Holeta & YRPH_Holeta
18	qYrS.54	7A	12800907-50346076	5	YRF_Kulumsa, YRH_Kulumsa, YRM_Kulumsa, YRMM_Kulumsa & YRF_Meraro
19	qYrS.55	7A	96563306-128909455	4	YRF_Holeta, YRH_Holeta, YRMM_Holeta & YRF_Meraro
20	qYrS.56	7D	9295305-14621383	3	YRH_Holeta, YRH_Holeta, YRH_Holeta, YRF_Holeta, & YRMM_Holeta

QTL= Quantitative trait locus; Chr = Chromosomes, Phenotype_Location = coefficient of infection measured at individual or across locations (Holetta, Kulumsa, and Meraro), YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity and YRM = coefficient of infection at maturity, *=QTLs stable across all environments and all growth stages

Even though it is challenging to compare the positions of QTLs from different studies because of the different mapping methodologies, marker systems, and mapping populations employed, some QTLs found in this study coincided with the mapping positions of previously reported yellow rust resistant genes in the literature. Similar to the current study, several earlier studies reported yellow rust-resistant QTLs on 1A (Fu et al., 2019; Tehseen et al., 2020; Yao et al., 2021; Baranwal et al., 2022; Bouvet et al., 2022), on 1B (Losert et al., 2017; Alemu et al., 2020; Baranwal et al., 2022), on 1D (Long et al., 2019; Jia et al., 2020; Zhang et al., 2021; Baranwal et al., 2022; Kumar et al., 2023), on 2A (Tehseen et al., 2020; Zhang et al., 2021; Baranwal et al., 2022; Zhang et al., 2021), on 2B (Li et al., 2020), on 2D (Mu et al., 2020; Baranwal et al., 2022), on 3A (Tehseen et al., 2022), on 3B (Zegeye et al., 2014; Kumar et al., 2020), on 3D (Bouvet et al., 2022), on 4A (Mu et al., 2020), on 4B (Alemu et al., 2020), on 4D (Rollar et al., 2021), on 5A (Zhang et al., 2021), on 5B (Lu et al., 2014), on 5D (Zhang et al., 2021), on 6A (Baranwal et al., 2022), on 6B (Zhang et al., 2021) on 7A (Yel et al., 2019; Alemu et al., 2020; Tehseen et al., 2020; Baranwal et al., 2022), and on 7D (Long et al., 2019; Rollar et al., 2021). Out of the 54 putative QTLs detected in the current study, 12 QTLs (qYrS.11 on chromosome 1D; qYrS.16, qYrS.17, and qYrS.18 on chromosome 1B; qYrS.26 on chromosome 3A; qYrS.31 and qYrS.32 on chromosome 3B; qYrS.40 on chromosome 4B; qYrS.45 and qYrS.46 on chromosome 5D; qYrS.50 on chromosome 6B; and qYrS.58 on chromosome 7D) were not reported in previous literature on wheat and hence could potentially be novel (Supplementary Table 9).

On chromosome 1A, the discovery of defense-related candidate genes like *TraesCS1A02G325400* and *TraesCS1D02G018500* on in the significant markers suggests that the observed QTL areas are functionally associated with plant defense mechanisms against fungal infections. Furthermore, genes such as *TraesCS1A02G183400*, found on the qYrS.02 QTL region on chromosome 1A, and *TraesCS1B02G480300*, found on the qYrS.08 QTL region on chromosome 1B, are

involved in plants' systemic acquired resistance to pathogen infections. According to Lawton et al., (1995), systemic acquired resistance is a broad-spectrum resistance acquired following the initial localized infection of plants by pathogens. Genes such as *TraesCS1B02G324300*, found in qYrS.07, and *TraesCS6B02G017900*, in the qYrS.49 region, on chromosome 1B and 6B, respectively, control the MAPK cascades that signal various defense reactions, such as the production of signaling of plant stress, gene activation, and hypersensitive response cell death.

Due to the lack of shared genetic effects for yellow rust resistance, the majority of the QTLs discovered for vegetative, yield-related, and phenological traits did not overlap with those discovered for yellow rust resistance traits. Numerous associations between agronomic traits and yellow rust resistance traits were non-significant, had minimal to weak negative coefficients, or were both, showing that the traits were independent. However, this study showed that some putative QTLs determined for agronomic traits and putative QTLs identified by yellow rust resistance data overlapped. For example, the potential QTL identified on 1B for grain yield was co-mapped with qYrS.07, identified for yellow rust resistance at the maturity stage. This implies that there may be a genetic link between grain yield and yellow rust resistance

The putative QTL determined for plant height on chromosome 2A is co-mapped with qYrS.12, identified for the resistance of yellow rust at flowering. That is consistent with the finding of Mekonnen et al., (2021), who stated that the putative QTL controlling grain yield is co-mapped with the *Septoria tritici* blotch progress coefficient on chromosome 1A. This also suggests that there may be a genetic link between traits related to plant height and disease resistance in wheat, which could have implications for breeding programs aimed at improving multiple traits at the same time.

CONCLUSION AND RECOMMENDATION

Conclusion

Wheat is a key food security crop in Ethiopia. High population growth and fast urbanization boosted wheat demand in Ethiopia, resulting in a massive imbalance between supply and consumption. This imbalance has led to increased wheat imports, making Ethiopia heavily dependent on foreign sources for its wheat supply. On the other hand, stripe rust is caused by *Puccinia striiformis*, a serious wheat output-limiting factor in Ethiopia and elsewhere. Stripe is a fungal disease that affects wheat crops and can cause significant yield losses. It spreads rapidly through wind and thrives in cool and humid conditions, which are common in Ethiopia's highland regions. Genetic resistance is regarded as the most effective, long-lasting, affordable, and ecologically benign means of disease prevention. Moreover, successful resistance breeding requires an understanding of virulence, infection patterns, and the identification and deployment of resistance sources.

The first objective of the present study was to investigate genetic diversity and population structure analysis of bread wheat genotypes as revealed by ISSR markers. All the ISSR loci were highly polymorphic in the studied population, and found to be very useful tool to successfully depict the genetic diversity and population structure of the bread wheat populations. The analysis revealed a substantial genetic diversity within the studied wheat populations, where 95% of the total genetic diversity was within populations. Among the eight studied populations, ISEPTON showed relatively higher Shannon's Information Index ($I=0.4$) and Ne's gene diversity, implying that it could serve as a good source of desirable genes for wheat improvement program. UPGMA based clustering, PCoA analysis, and STRUCTURE analysis inadequately grouped the populations, confirming high genetic intermixing and high gene flow among populations. The STRUCTURE analysis confirmed the studied bread wheat populations shared genetic background that originated from three sub-populations. This data is very helpful for wheat breeders to gain a better understanding of the genetic diversity and population structure of wheat in Ethiopia, which will be useful in producing superior varieties and adopting effective conservation policies.

The other portion of the study focused on exploring the genetic variability of 180 bread wheat genotypes based on 12 agro-morphological traits. Wide variability was identified

among the tested bread wheat genotypes. This implies that the phenotypic difference designates a promising possibility to improve desired traits using genetic variability. Moreover, traits such as plant height, number of kernels per spike, thousand kernel weight, and spike weight had considerable heritability and genetic advance as percent of mean. Selection of germplasm based on these traits can result in worthy improvements in wheat breeding programs. The direct and indirect effects of various traits on grain yield per plot could be considered suitable as selection criteria for the development of high-yielding bread wheat varieties. Moreover, the majority of agronomic traits investigated had moderate to high heritability, indicating the presence of breeding-relevant genes. This suggests that breeding efforts have the ability to target and select for these traits, resulting in increased grain output in future generations. Furthermore, the high heritability indicates that these features are substantially impacted by genetic factors, making them appropriate targets for selection and breeding efforts. The GGE biplot analysis also confirmed the existence of a genotype-environment interaction for grain yield performance, suggesting that the performance of different genotypes varied across different environments. This indicates that certain genotypes may be better suited for specific environmental conditions, while others may perform well in a wider range of environments. AMMI and GGE biplot analyses showed that genotypes G58, G168, G53, and G68 are corner genotypes suited to particular environments. The GE interaction for grain yield in this wheat MET also indicates the presence of differentially adapted wheat genotypes. Since there is enormous opportunity for improving bread wheat germplasm, the data acquired from this study can be used by breeders to who the studied traits are of interest or relevant.

In addition, the present study besides looked at the virulence patterns of four Ethiopian *P. striiformis* isolates collected from typical stripe rust hotspot areas. The isolates were inoculated onto a collection of differential wheat cultivars with known resistance genes to assess pathogenicity patterns. The study revealed that Ethiopian *P. striiformis* isolates exhibit broad-spectrum virulence on bread wheat germplasm. The isolates that were determined to be highly virulent could be used for germplasm screening in a resistance breeding effort. The Yr15 gene in K-6290-Bulk exhibits broad-spectrum resistance to *P. striiformis* isolates, suggesting potential use for developing high-yielding yet stripe-rust-susceptible wheat cultivars. The findings shed light on the pathogenicity spectrum of Ethiopian *P. striiformis* populations, the effectiveness of Yr

genes, and the resistance status of wheat genotypes; consenting breeders to better understand the dynamics of wheat *P. striiformis* interactions in Ethiopia. This knowledge can notify breeding programs and help develop more resistant wheat varieties to combat the devastating effects of stripe rust in the region.

Genomic regions underlying adult-plant resistances to yellow rust were explored using genome-wide scanned SNPs and multi-environment-derived phenotype data in the bread wheat association panel. Besides, 6788, high-density DArTSeq SNPs were utilized to investigate the population structure, LD, and genetic architecture of adult-plant resistance to stripe rust in 178 bread wheat genotypes. At three different locations, the association panel was phenotyped for stripe rust resistance, phenology, yield, and yield-related characteristics. Furthermore, genotypes G3, G13, G37, G53, G72, G87, G92, G93, G157, and G174 were among the top 5% best stripe rust-resistant genotypes, with 70.36-75.16 % super resistance to the moderately resistant standard check Kingbird and 71.09-58.38% over the average of 13 released varieties. These genotypes have outperformed both the standard check Kingbird and the average resistance of other released varieties in Ethiopia in terms of stripe rust resistance. This implies that they might be candidates for future breeding initiatives targeted at producing variants that are even more resistant.

This study identified several significant genomic regions associated with adult-plant resistance to yellow rust. The analysis revealed that yellow rust resistance is highly heritable ($h^2 = 60\%$), suggesting that resistance to stripe rust is strongly influenced by genetics. Moreover, the structure analysis revealed three subpopulations with a greater degree of genetic mixing in the association panel. The genetic backgrounds of these subpopulations were heterogeneous, indicating some ancestral sources within the association panel. The linkage disequilibrium between the markers and genes contributing to stripe rust resistance decreased to $r^2 = 0.2$ at a physical distance of 36.88–218.80 Mbp in all chromosomes, with an overall mean of 31.44 Mbp. This shows the presence of genetically linked markers and genes responsible for stripe rust resistance are genetically linked. However, the vast majority of physical distances at which linkage disequilibrium reduces suggest that these markers and genes are dispersed across sub-genomes and chromosomes.

The study also found 148 SNPs that were significantly associated with strong yellow rust resistance, pointing to 54 QTLs. Some of these putative QTLs were consistently identified at all growth stages, and hence, they could be considered major genomic loci containing combinations of genes conferring resistance to *P. striiformis* across all growth stages. Most of the detected resistance QTLs were located on the same chromosomes as previously reported QTLs for yellow rust resistance and mapped on chromosomes 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 6A, 6B, and 7A and 7D. However, 12 of the detected MTAs have never been recorded in the wheat literature, indicating that they might be novel loci for stripe rust resistance.

Zooming the observed loci on IWGSC RefSeq Annotation v2.1 designated the existence of disease resistance-associated genes in the identified QTL areas. Three of the stripe rust resistances QTLs were discovered to be co-localized with agronomic trait MTAs. This co-localization supports an agronomic traits impact, on stripe rust resistance. Additionally, more research on agronomic traits needed to understand the underlying processes and their possible consequences for breeding efforts.

Functional dissection of the detected QTL region in the wheat database identified several defense-related candidate genes involved in plant resistances against fungal infections, systemic acquired resistance, and MAPK pathways that are relevant in signaling numerous plant defense systems. The identified candidate genes close to the detected SNPs can be targeted to disclose the actual genes underlying the target trait in the association loci. Most of the detected putative QTLs shared similar chromosomal positions with previously reported QTLs. Essentially; the study confirmed that the association panel possessed considerable *P. striiformis* resistance alleles that could be deployed into the high-yielding but yellow rust-susceptible wheat varieties. Overall, the association research was successful in revealing the genetic architecture of adult-plant resistance to stripe rust resistance. The stable resistant wheat genotypes and QTLs found might be used in wheat breeding to generate long-lasting and broad-spectrum resistance variants against *P. striiformis*. These resistant varieties may lower the need for chemical pesticides while increasing crop yields, resulting in more sustainable, environmental friendly and economically viable wheat production methods.

Finally, this study describes the amount and patterns of genetic diversity, population structure, heritability, genotype-environment interaction of bread wheat genotypes, virulence variability of the devastating wheat pathogen *P. striiformis*, and adult plant genomic regions associated with stripe rust resistance in bread wheat genotypes. It also reports promising high-yielding and stable stripe rust resistance sources, qualitative resistance genes (Yr genes), and QTLs important for the long-term and effective control of stripe rust disease in wheat in Ethiopia, resulting in increased and stable wheat production and productivity that contribute to food and nutritional security as well as overall economic progress.

Recommendations

The overall findings of this study allowed for better yield and stripe rust resistance-breeding strategies could be developed to enhance bread wheat productivity and protect against stripe rust outbreaks. Additionally, it would be beneficial to consider it as a source of genetic material for the crossing of desired traits, such as enhancing yield and stripe rust resistance. Accordingly, the major recommendations and directions for future research are:

1. To generate a better insight in genetic diversity and population structure of bread wheat genotypes and for development of best-performing cultivars, further research using high-density marker such as SNP markers that includes large sets of bread wheat genotypes in the country is recommended.
2. As this study was done in three environments over the course of one season, further research is recommended to explore the long-term effects of different seasons and additional environments on the findings
3. Additionally, any future research on *P. striiformis* genetic diversity by including additional numerous isolates from the already-known hotspot areas, such as the Shewa and Bale areas will provide researchers with better knowledge of the pathogen's genetic diversity and potential for further dissemination.
4. In addition, it would be important to investigate the environmental factors that contribute to the development and spread of *P. striiformis*. Understanding how these factors interact with genetic diversity can help inform strategies for disease management and prevention.

5. The efficacy of newly found QTLs need functionally confirmed before they can be used for marker-assisted selection.
6. Moreover, as stripe rust can travel more than 800 kilometers, it is crucial to establish collaborations with other countries and institutions to ensure a comprehensive understanding of the stripe rust spread and its effective monitoring on a regional scale. This would allow to develop early warning systems and implement coordinated strategies for prevention and control

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APPENDICES (SUPPLEMENTARY MATERIALS)

Supplementary tables

Supplementary table 1. Field layouts and Sowing for each location in 2020 with two replications.

Cod e	Location	Plots	Design	Geographic position (Latitude/ Longitude)		Altitude	Average rainfall	Temperature range	Planting date	Soil type
E1	Holeta	180	(14 entries/block × 11 blocks) × 2 reps	38°30' E	9° 00' N	2990 masl	1144 mm	6-22°C	04/07/2020	Clay and vertisols soil
E2	Kulumsa	180	(14 entries/block × 11 blocks) × 2 reps	39° 09' 11" E	08° 01' 10" N	2200 m.a.s.l.	840 mm	10-22°C	11/07/2020	Clay soil
E3	Meraro	180	(14 entries/block × 11 blocks) × 2 reps	39° 14'56"E	07° 24' 27"N	2400 m.a.s.l.	1096 mm	5.7-18.1°C	18/06/2020	Clay soil

Supplementary table 2. Mean and standard deviation of disease severity and seedling response across 180 wheat genotypes

Geno types	N	Disease severity				Seedling response			
		Deka isolate	Hidasia isolate	Meraro isolate	Senatia isolate	Deka isolate	Hidasia isolate	Meraro isolate	Senatia isolate
		M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD
G1	2	2±0	1±1.42	1.5±0.71	0.5±0.71	1±1.42	1.5±2.13	1.5±0.71	0.5±0.71
G2	2	1.5±0.71	2.5±0.71	1±0	1.5±2.13	1.5±0.71	2.5±0.71	1±0	2±2.83
G3	2	2±0	4.5±0.71	1±1.42	2±2.83	2±0	4±0	0.5±0.71	2±2.83
G4	2	3±0	2.5±0.71	1.5±0.71	1±0	2.5±0.71	3±1.42	1.5±0.71	1±0
G5	2	1.5±0.71	3±1.42	2±0	2±2.83	1±1.42	3.5±2.13	2±0	2±2.83
G6	2	4±0	5±0	4±1.42	3.5±2.54	3.5±0.71	4±0	3.5±0.71	3±2.83
G7	2	2.5±0.71	2.5±0.71	2.5±0.71	1.5±0.71	1.5±2.13	2.5±0.71	3±1.42	1±1.42
G8	2	3±0	1±1.42	1±0	1.5±2.13	2.5±0.71	1±1.42	1±0	2±2.83
G11	2	4±1.42	4.5±0.71	3±1.42	4±1.42	3.5±0.71	4±0	3±1.42	3.5±0.71
G12	2	3.5±0.71	2.5±3.54	2±1.42	4.5±6.37	3.5±0.71	2±2.83	0.5±0.71	2.5±3.54
G13	2	3±0	3.5±2.13	2±1.42	5±5.66	2.5±0.71	3±1.42	2±1.42	3±2.83
G15	2	1±0	1.5±2.13	1±1.42	3.5±2.13	0.5±0.71	1.5±2.13	1±1.42	3±1.42
G16	2	3.5±0.71	5.5±0.71	2.5±3.54	3±4.25	3±1.42	4±0	2±2.83	2±2.83
G17	2	2.5±0.71	2.5±0.71	1±0	1±0	2.5±0.71	2.5±0.71	1±0	1±0
G18	2	3±0	4±2.83	4±1.42	3±1.42	2.5±0.71	3±1.42	3.5±0.71	3±1.42
G19	2	4±1.42	2±0	2.5±0.71	2.5±3.54	3.5±0.71	2±0	2.5±0.71	2±2.83
G20	2	0.5±0.71	2±0	0±0	1.5±0.71	0.5±0.71	2±0	0±0	1.5±0.71
G23	2	3.5±0.71	3±1.42	1.5±2.13	6.5±3.54	3.5±0.71	2±0	0±0	4±0
G24	2	3±1.42	2.5±0.71	1.5±0.71	4±1.42	3±1.42	2.5±0.71	1.5±0.71	3.5±0.71
G25	2	2±0	1.5±0.71	1±1.42	1.5±0.71	3±1.42	1.5±0.71	0±0	1.5±0.71
G26	2	2.5±0.71	3±0	1.5±0.71	1±1.42	2.5±0.71	3±0	1.5±0.71	1±1.42
G27	2	2±0	2±0	1.5±0.71	1.5±0.71	1±1.42	2±0	1.5±0.71	1.5±0.71
G28	2	2.5±0.71	2±1.42	1.5±0.71	1.5±0.71	2.5±0.71	2.5±2.13	1±0	1.5±0.71
G29	2	4±0	3.5±2.13	5±5.66	3±2.83	4±0	3±1.42	3±2.83	2.5±2.13
G30	2	4.5±2.13	2.5±0.71	2±2.83	3±2.83	3.5±0.71	2.5±0.71	2±2.83	2.5±2.13
G31	2	4±1.42	6.5±3.54	3.5±3.54	4±1.42	3.5±0.71	4.5±0.71	3.5±2.13	3.5±0.71
G34	2	3±0	3±0	5±5.66	4±0	3±0	2.5±0.71	3±2.83	4±0
G35	2	3±0	5±1.42	2±1.42	2.5±3.54	1.5±2.13	4±0	2±1.42	2±2.83
G36	2	2±0	3±1.42	1.5±0.71	3±2.83	1±1.42	3±1.42	1±0	2.5±2.13
G37	2	2±0	3.5±0.71	1.5±2.13	1.5±2.13	1±1.42	3.5±0.71	1.5±2.13	1.5±2.13
G38	2	2±0	2±0	1±1.42	3±2.83	2±0	1±1.42	1±1.42	2.5±2.13
G39	2	2±0	2.5±0.71	2±0	2±1.42	1±1.42	2.5±0.71	2±0	2±1.42
G41	2	1±1.42	1±1.42	1±1.42	1.5±0.71	1±1.42	1.5±2.13	1±1.42	1.5±0.71
G42	2	4±1.42	2.5±0.71	3.5±0.71	3±2.83	3.5±0.71	2.5±0.71	2.5±2.13	2.5±2.13
G43	2	4±1.42	2.5±0.71	2±0	2.5±2.13	3.5±0.71	2.5±0.71	2±0	2.5±2.13
G44	2	1±0	1.5±0.71	2±0	1.5±0.71	0.5±0.71	1.5±0.71	2.5±0.71	1.5±0.71
G45	2	2±0	3±1.42	3±0	2.5±3.54	1±1.42	3±1.42	3±0	2±2.83
G46	2	1.5±0.71	0±0	1.5±0.71	2±1.42	1.5±0.71	0±0	1.5±0.71	2.5±2.13
G47	2	2.5±0.71	1±1.42	2.5±0.71	4.5±0.71	1.5±2.13	1±1.42	2.5±0.71	4±0
G48	2	1±0	1±1.42	2±0	4±1.42	0.5±0.71	1±1.42	2±0	4±0
G49	2	1±0	2.5±0.71	3±0	2±1.42	0.5±0.71	1.5±2.13	3±0	2.5±2.13
G50	2	1±0	0.5±0.71	1±1.42	2.5±0.71	0.5±0.71	0.5±0.71	1±1.42	2±1.42

G51	2	4±1.42	2±0	4±1.42	3±2.83	3.5±0.71	1±1.42	3±1.42	2.5±2.13
G52	2	2.5±0.71	2±0	3±1.42	2±2.83	2.5±0.71	1±1.42	2.5±2.13	2±2.83
G53	2	1.5±0.71	1.5±0.71	1.5±0.71	2±1.42	1.5±0.71	1±1.42	1.5±0.71	2.5±2.13
G54	2	3.5±2.13	2.5±0.71	3.5±0.71	2.5±3.54	3±1.42	2.5±0.71	3±1.42	2±2.83
G55	2	1±0	3±1.42	3.5±2.13	4±1.42	1±0	3±1.42	3±1.42	3.5±0.71
G56	2	2±0	2.5±0.71	3±1.42	3.5±0.71	1±1.42	1.5±2.13	3±1.42	3.5±0.71
G57	2	2±0	2.5±0.71	5±0	4±0	1.5±0.71	1.5±2.13	2.5±2.13	4±0
G58	2	4.5±0.71	2.5±0.71	2±0	3±0	4.5±0.71	2.5±0.71	1±1.42	3±0
G59	2	2±0	3.5±0.71	3±2.83	4±1.42	1±1.42	3.5±0.71	2.5±2.13	2.5±2.13
G60	2	4±1.42	2.5±0.71	4.5±0.71	3±0	3.5±0.71	2.5±0.71	4±0	2±1.42
G61	2	1.5±0.71	3±0	2.5±0.71	2.5±0.71	1.5±0.71	3.5±0.71	2.5±0.71	1.5±2.13
G62	2	1.5±0.71	2±1.42	1±0	1±0	1.5±0.71	2±1.42	1±0	1±0
G63	2	1.5±0.71	3±0	1±1.42	1.5±0.71	1±1.42	3.5±0.71	1±1.42	1.5±0.71
G64	2	2±0	4.5±0.71	2±0	2.5±0.71	2±0	2.5±2.13	1.5±0.71	2.5±0.71
G65	2	1±0	2±0	0.5±0.71	2.5±0.71	0.5±0.71	3±1.42	0±0	2±1.42
G66	2	2.5±0.71	1.5±0.71	1±0	2.5±0.71	2.5±0.71	1.5±0.71	1±0	2±1.42
G67	2	0±0	2.5±0.71	1±0	1±0	0±0	1.5±2.13	1±0	1±0
G68	2	1.5±0.71	2±1.42	0.5±0.71	3±0	1±1.42	2±1.42	0±0	3±0
G69	2	2±0	3±1.42	3±2.83	4±1.42	1±1.42	2±2.83	3±2.83	3.5±0.71
G70	2	2±0	2.5±0.71	3.5±2.13	3±1.42	1±1.42	1.5±2.13	3±1.42	3±1.42
G73	2	1.5±0.71	1.5±0.71	1.5±0.71	3±1.42	1.5±0.71	1.5±0.71	1.5±0.71	3±1.42
G74	2	0±0	2±0	1.5±0.71	1±1.42	0±0	2±0	1.5±0.71	1±1.42
G75	2	2±0	2.5±0.71	4±1.42	2.5±0.71	1±1.42	2.5±0.71	3.5±0.71	2.5±0.71
G76	2	0.5±0.71	2.5±0.71	1±0	4±2.83	0.5±0.71	1.5±2.13	1±0	3.5±2.13
G77	2	0.5±0.71	1.5±0.71	1±0	1.5±0.71	0.5±0.71	1±1.42	1±0	2±1.42
G78	2	1±0	2.5±0.71	0.5±0.71	2±1.42	0.5±0.71	1.5±2.13	0.5±0.71	2.5±2.13
G79	2	1.5±0.71	2±1.42	1.5±0.71	3.5±2.13	1±1.42	1.5±2.13	1.5±0.71	4±0
G81	2	2±0	3±1.42	1.5±0.71	4±1.42	2±0	2±2.83	0.5±0.71	4±0
G83	2	1.5±0.71	2.5±0.71	1.5±0.71	3±0	1.5±0.71	1.5±2.13	1.5±0.71	3±0
G84	2	0±0	0±0	1±1.42	1.5±0.71	0±0	0±0	1±1.42	2±1.42
G85	2	0±0	2.5±0.71	1±1.42	1.5±0.71	0±0	2.5±0.71	1±1.42	2±1.42
G86	2	0±0	2.5±0.71	1.5±0.71	0±0	0±0	1.5±2.13	1.5±0.71	0±0
G87	2	4±1.42	3.5±0.71	1.5±0.71	3.5±0.71	3.5±0.71	2±2.83	1.5±0.71	3±1.42
G88	2	0.5±0.71	2.5±0.71	0.5±0.71	0.5±0.71	0.5±0.71	1.5±2.13	0.5±0.71	0.5±0.71
G89	2	2±0	3±1.42	3±1.42	3.5±0.71	1.5±0.71	2.5±2.13	2.5±2.13	3±1.42
G90	2	2±0	4±1.42	3.5±2.13	3±1.42	1±1.42	2±2.83	2.5±2.13	3±1.42
G91	2	3±0	3.5±0.71	4.5±2.13	5.5±0.71	4.5±0.71	5±2.83	3.5±0.71	4±1.42
G92	2	1.5±0.71	1.5±0.71	3±1.42	0.5±0.71	1.5±0.71	1±1.42	2±2.83	0.5±0.71
G93	2	1.5±0.71	3±1.42	0±0	0.5±0.71	2±1.42	2±2.83	0±0	0.5±0.71
G94	2	2±0	4±1.42	2±0	3.5±0.71	2±0	2±2.83	1±1.42	3.5±0.71
G97	2	2±0	3±0	4.5±0.71	3±0	1±1.42	3±0	4±0	3±0
G98	2	1.5±0.71	2±0	1.5±0.71	1.5±0.71	1.5±0.71	3±1.42	1.5±0.71	1.5±0.71
G99	2	4±1.42	4.5±0.71	4.5±0.71	4±1.42	3.5±0.71	4±0	4±0	3.5±0.71
G100	2	2±0	4±1.42	2±0	5±0	2±0	3.5±0.71	2±0	4±0
G101	2	3±0	4±1.42	4.5±0.71	5.5±0.71	2.5±0.71	2±2.83	3.5±0.71	3.5±2.13
G102	2	0±0	1.5±0.71	1±0	1.5±0.71	0±0	1±1.42	1±0	1.5±0.71
G103	2	0.5±0.71	3±1.42	0±0	1±1.42	0.5±0.71	2±2.83	0±0	1±1.42
G104	2	1.5±0.71	1.5±0.71	1.5±0.71	4±2.83	1.5±0.71	1±1.42	1±1.42	2.5±3.54
G105	2	3±0	3±0	3±0	6±0	3±0	2±1.42	3±0	4.5±0.71

G106	2	2±0	1.5±0.71	3±1.42	4±0	2±0	1±1.42	2.5±2.13	4±0
G107	2	2.5±0.71	2.5±0.71	2.5±0.71	4.5±0.71	2.5±0.71	2.5±0.71	1.5±2.13	3.5±0.71
G108	2	5±1.42	4±1.42	2±0	4.5±0.71	4±0	2±2.83	2±0	4±0
G109	2	4±1.42	4±1.42	4±1.42	4.5±2.13	3.5±0.71	2±2.83	2±2.83	4±1.42
G110	2	2±0	4±1.42	2.5±0.71	4±1.42	1±1.42	2±2.83	2.5±0.71	3.5±0.71
G111	2	2±0	3±1.42	3.5±2.13	5±0	2±0	2±2.83	3±1.42	4±0
G112	2	3±0	1.5±0.71	1.5±0.71	1±0	3.5±0.71	1±1.42	1.5±0.71	1±0
G113	2	3±0	2±0	1.5±0.71	3±0	3.5±0.71	1±1.42	0.5±0.71	3±0
G114	2	3.5±2.13	4±1.42	1±1.42	2.5±0.71	3±1.42	2±2.83	0±0	2.5±0.71
G115	2	5±1.42	1.5±0.71	2.5±0.71	4.5±0.71	4±0	1±1.42	2.5±0.71	3.5±0.71
G116	2	1.5±0.71	1.5±0.71	0.5±0.71	4±2.83	1.5±0.71	1±1.42	0.5±0.71	2.5±3.54
G117	2	3±0	2±0	4±1.42	6±0	2.5±0.71	1±1.42	3.5±0.71	4.5±0.71
G118	2	1.5±0.71	2±1.42	1±0	2.5±0.71	1.5±0.71	1.5±2.13	0.5±0.71	1.5±2.13
G119	2	2±0	0.5±0.71	1.5±0.71	4±1.42	2±0	0±0	1±1.42	4±0
G120	2	3.5±2.13	2.5±0.71	1±1.42	4.5±0.71	3±1.42	1.5±2.13	0.5±0.71	2±2.83
G121	2	5±1.42	3.5±2.13	1.5±2.13	5.5±0.71	4±0	3±1.42	0±0	4±0
G122	2	2±0	4±1.42	1±1.42	5±0	2±0	3.5±0.71	1±1.42	2±2.83
G123	2	3.5±0.71	1.5±2.13	1±1.42	5±1.42	3.5±0.71	1.5±2.13	0.5±0.71	2.5±3.54
G124	2	2.5±0.71	3±0	1.5±2.13	5±0	2.5±0.71	3±0	2.5±3.54	2±2.83
G125	2	1±0	1±1.42	1±1.42	2.5±0.71	1±0	1±1.42	1±1.42	1.5±2.13
G126	2	0±0	0±0	0.5±0.71	3.5±2.13	0±0	0±0	0.5±0.71	2±2.83
G128	2	2±0	4±1.42	1.5±0.71	3±1.42	2±0	3.5±0.71	1±0	3±1.42
G129	2	5±1.42	4±1.42	1.5±2.13	4±1.42	4±0	3.5±0.71	0.5±0.71	3±1.42
G130	2	2.5±0.71	3.5±0.71	2±1.42	5±1.42	2.5±0.71	3±1.42	1±0	3±2.83
G131	2	2.5±0.71	4±2.83	1.5±2.13	5±0	2.5±0.71	3±1.42	0.5±0.71	4±0
G133	2	4.5±0.71	2±0	1±1.42	4.5±0.71	4±0	2±0	0±0	3±1.42
G134	2	4.5±0.71	4±0	1.5±2.13	4.5±0.71	4±0	3.5±0.71	0±0	4±0
G136	2	3±0	2.5±0.71	1±1.42	3.5±0.71	3±0	2.5±0.71	0.5±0.71	3±1.42
G137	2	2±0	4.5±0.71	1.5±0.71	5±0	2±0	2±2.83	1±0	3±1.42
G138	2	2.5±0.71	0.5±0.71	0.5±0.71	2.5±0.71	1.5±2.13	0.5±0.71	0±0	1.5±2.13
G139	2	3±1.42	2.5±0.71	0.5±0.71	2.5±0.71	3±1.42	2±1.42	1.5±0.71	2.5±0.71
G140	2	3.5±2.13	2.5±0.71	1±1.42	4.5±0.71	3±1.42	2.5±0.71	1±1.42	3±1.42
G141	2	3.5±2.13	2±2.83	1±1.42	5±0	3±1.42	2±2.83	2±1.42	3.5±0.71
G142	2	2±0	2.5±3.54	1.5±0.71	5±0	2±0	2±2.83	1.5±0.71	4±0
G144	2	3±0	3±0	1±0	2.5±0.71	3.5±0.71	3±0	1±0	2±1.42
G145	2	2±1.42	1.5±2.13	0.5±0.71	3.5±2.13	2±1.42	1.5±2.13	1±1.42	4±0
G146	2	3±0	4.5±2.13	1.5±0.71	4.5±0.71	1.5±2.13	4±1.42	1.5±0.71	4±0
G147	2	5±1.42	3±1.42	1±1.42	4.5±0.71	4±0	3±1.42	0.5±0.71	3.5±0.71
G148	2	2±0	3.5±2.13	1±1.42	3±0	1±1.42	3±1.42	0.5±0.71	3±0
G150	2	5±0	2.5±0.71	1±1.42	4±1.42	4±0	2.5±0.71	0±0	3.5±0.71
G151	2	2.5±0.71	1.5±2.13	1±1.42	3±0	2.5±0.71	1.5±2.13	0±0	3±0
G153	2	2.5±0.71	2.5±0.71	0.5±0.71	3±1.42	3±1.42	2.5±0.71	2±2.83	2±2.83
G154	2	4±2.83	2±2.83	1±1.42	2.5±0.71	3±1.42	2±2.83	1.5±0.71	2±1.42
G155	2	2.5±0.71	1±1.42	0.5±0.71	2.5±0.71	2.5±0.71	1±1.42	0±0	2.5±0.71
G156	2	4.5±2.13	2.5±0.71	1.5±2.13	5±0	3.5±0.71	2.5±0.71	0.5±0.71	2±2.83
G158	2	5±1.42	2.5±0.71	1.5±2.13	2±1.42	4±0	2.5±0.71	0.5±0.71	0.5±0.71
G159	2	3±0	1±1.42	0.5±0.71	0.5±0.71	3.5±0.71	0.5±0.71	0±0	0±0
G160	2	2±0	1±1.42	0±0	0.5±0.71	3±1.42	1±1.42	1±0	0.5±0.71
G161	2	3.5±0.71	1.5±2.13	1±1.42	2.5±0.71	3.5±0.71	1.5±2.13	0±0	2.5±0.71

G162	2	5±1.42	2±2.83	1.5±2.13	4.5±0.71	4±0	2±2.83	1±0	3±1.42
G163	2	4±1.42	3.5±2.13	1±1.42	1±1.42	3.5±0.71	3±1.42	0.5±0.71	1±1.42
G164	2	2.5±0.71	2±0	0.5±0.71	3±0	2.5±0.71	2±0	0.5±0.71	3±0
G166	2	2.5±0.71	1.5±2.13	0.5±0.71	2.5±0.71	3.5±0.71	1.5±2.13	0.5±0.71	2.5±0.71
G167	2	2±0	1.5±0.71	2±2.83	4.5±0.71	2±0	1.5±0.71	0±0	3±1.42
G168	2	3±0	1.5±2.13	0.5±0.71	1±1.42	3±0	1.5±2.13	1±0	1±1.42
G169	2	2±0	1±1.42	0±0	1±0	3±1.42	1±1.42	0±0	1±0
G170	2	4±1.42	1.5±2.13	1±1.42	5±0	3.5±0.71	1.5±2.13	1.5±0.71	3±1.42
G171	2	5±1.42	1.5±2.13	0.5±0.71	2.5±0.71	4±0	1.5±2.13	1±0	2.5±0.71
G172	2	4±1.42	2.5±3.54	1±1.42	5.5±0.71	3.5±0.71	2±2.83	0.5±0.71	3±2.83
G174	2	2.5±0.71	1±1.42	1.5±2.13	2.5±0.71	2.5±0.71	1±1.42	0±0	2±1.42
G176	2	4±1.42	2.5±0.71	1±1.42	1.5±0.71	3.5±0.71	3±1.42	0±0	1.5±0.71
G177	2	0±0	1±1.42	0±0	0±0	0±0	1±1.42	1±1.42	0±0
G178	2	2±0	3.5±2.13	1.5±0.71	1.5±0.71	2±0	3.5±0.71	2.5±2.13	1±1.42
G179	2	1.5±0.71	1.5±2.13	1±1.42	0.5±0.71	1±1.42	1.5±2.13	1±1.42	0.5±0.71
G180	2	1.5±0.71	1.5±0.71	0.5±0.71	0.5±0.71	1±1.42	1±1.42	1.5±0.71	0.5±0.71

Supplementary table 3. Coefficient of infection of Deka, Hidasia, Meraro and Senatia isolates in 180 bread wheat genotypes

Genotypes	Coefficient of infection				Average
	Deka isolate	Hidasia isolate	Meraro isolate	Senatia isolate	
G1	0.40	0.23	0.23	0.10	0.225
G2	0.23	0.63	0.10	0.90	0.4
G3	0.40	2.03	0.40	0.90	0.826563
G4	0.90	0.90	0.23	0.10	0.451563
G5	0.23	1.60	0.40	0.90	0.689063
G6	1.90	2.50	2.60	1.60	2.33
G7	0.63	0.63	0.63	0.23	0.50625
G8	0.90	0.23	0.10	0.63	0.4
G11	1.60	2.03	1.60	1.60	1.701563
G12	1.23	1.60	0.90	4.23	1.80625
G13	0.90	1.60	0.90	3.60	1.6
G15	0.10	0.63	0.23	0.63	0.351563
G16	1.23	3.03	1.60	2.03	1.914063
G17	0.63	0.63	0.10	0.10	0.30625
G18	0.90	2.50	1.60	0.90	1.40625
G19	1.60	0.40	0.63	1.60	0.976563
G20	0.03	0.40	0.00	0.23	0.1
G23	1.23	1.60	0.90	4.90	1.914063
G24	0.90	0.63	0.40	1.60	0.826563
G25	0.40	0.23	0.23	0.23	0.264063
G26	0.63	0.90	0.23	0.23	0.451563
G27	0.40	0.40	0.23	0.23	0.30625
G28	0.63	0.90	0.23	0.23	0.451563
G29	1.60	2.03	4.23	2.03	2.376563
G30	2.03	0.90	1.23	1.60	1.40625
G31	3.60	4.23	2.50	1.60	2.976563
G34	0.90	0.90	4.90	1.60	1.80625

G35	0.90	2.50	0.90	1.60	1.40625
G36	0.40	0.90	0.40	1.60	0.75625
G37	0.40	1.23	0.63	0.63	0.689063
G38	0.40	0.40	0.40	1.60	0.625
G39	0.40	0.63	0.40	0.63	0.50625
G41	0.10	0.40	0.10	0.23	0.189063
G42	1.60	0.90	1.23	1.60	1.314063
G43	1.60	0.63	0.40	0.90	0.826563
G44	0.10	0.23	0.40	0.23	0.225
G45	0.40	1.60	0.90	1.60	1.05625
G46	0.23	0.00	0.23	0.90	0.225
G47	0.63	0.40	0.63	2.03	0.826563
G48	0.10	0.23	0.40	0.90	0.351563
G49	0.10	0.63	0.90	0.90	0.564063
G50	0.10	0.03	0.10	0.40	0.126563
G51	1.60	0.40	1.60	1.60	1.225
G52	0.63	0.40	0.90	1.23	0.75625
G53	0.23	0.23	0.23	0.90	0.351563
G54	1.23	0.63	1.23	1.60	1.139063
G55	0.10	0.90	1.23	1.60	0.826563
G56	0.40	0.63	1.23	1.23	0.826563
G57	0.40	0.63	2.50	1.60	1.139063
G58	2.03	0.63	0.40	0.90	0.9
G59	0.40	1.23	1.60	1.60	1.139063
G60	1.60	0.63	2.03	0.90	1.225
G61	0.23	0.90	0.63	0.63	0.564063
G62	0.23	0.40	0.10	0.10	0.189063
G63	0.23	0.90	0.23	0.23	0.351563
G64	0.40	2.03	0.40	0.63	0.75625
G65	0.10	0.63	0.10	0.63	0.30625
G66	0.63	0.23	0.10	0.63	0.351563
G67	0.00	0.40	0.10	0.10	0.1
G68	0.23	0.40	0.10	0.90	0.351563
G69	0.40	0.90	2.50	2.03	1.314063
G70	0.40	0.63	1.60	0.90	0.826563
G73	0.23	0.23	0.23	0.90	0.351563
G74	0.00	0.40	0.23	0.23	0.15625
G75	0.40	0.63	1.23	0.63	0.689063
G76	0.03	0.40	0.10	0.40	0.189063
G77	0.03	0.23	0.10	0.23	0.126563
G78	0.10	0.63	0.10	0.63	0.30625
G79	0.23	0.40	0.23	0.63	0.351563
G81	0.40	0.90	0.40	1.60	0.75625
G83	0.23	0.63	0.23	0.90	0.451563
G84	0.00	0.00	0.23	0.40	0.076563
G85	0.00	0.40	0.23	0.40	0.189063
G86	0.00	0.63	0.23	0.00	0.1
G87	1.60	1.23	0.40	1.23	1.05625
G88	0.03	0.40	0.03	0.03	0.076563
G89	0.40	0.90	0.90	1.23	0.826563
G90	0.40	1.60	1.23	0.90	0.976563
G91	2.90	3.23	2.50	4.90	3.389063

G92	0.23	0.23	0.40	0.03	0.189063
G93	0.23	0.40	0.00	0.03	0.1
G94	0.40	1.60	0.40	1.23	0.826563
G97	0.40	0.90	2.03	0.90	0.976563
G98	0.23	0.40	0.23	0.23	0.264063
G99	1.60	2.03	2.03	1.60	1.80625
G100	0.40	1.60	0.40	2.50	1.05625
G101	0.90	1.60	2.50	4.90	2.25625
G102	0.00	0.23	0.10	0.23	0.1
G103	0.03	0.40	0.00	0.23	0.1
G104	0.23	0.23	0.23	0.63	0.30625
G105	0.90	0.90	0.90	5.63	1.701563
G106	0.40	0.23	0.90	1.60	0.689063
G107	0.63	0.63	0.63	1.60	0.826563
G108	2.50	1.60	0.40	2.03	1.501563
G109	1.60	1.60	1.60	3.60	2.025
G110	0.40	1.60	0.63	1.60	0.976563
G111	0.40	0.90	1.60	3.03	1.314063
G112	0.90	0.23	0.23	0.10	0.30625
G113	0.90	0.40	0.40	0.90	0.625
G114	1.23	1.60	0.40	0.63	0.9
G115	2.50	0.23	0.63	2.50	1.225
G116	0.23	0.23	0.10	0.63	0.264063
G117	0.90	0.40	1.60	3.60	1.40625
G118	0.23	0.40	0.10	0.63	0.30625
G119	0.40	0.10	0.23	0.90	0.351563
G120	1.23	0.63	0.40	2.50	1.05625
G121	2.50	1.60	0.90	3.60	2.025
G122	0.40	1.60	0.40	2.50	1.05625
G123	1.23	0.63	0.40	1.60	0.9
G124	0.63	0.90	0.63	2.50	1.05625
G125	0.10	0.23	0.23	0.63	0.264063
G126	0.00	0.00	0.03	0.40	0.039063
G128	0.40	1.23	0.40	0.63	0.625
G129	2.50	1.60	0.90	1.60	1.6
G130	0.63	1.23	0.90	4.23	1.501563
G131	0.63	2.50	0.90	2.50	1.501563
G133	2.03	0.40	0.40	2.03	1.05625
G134	2.03	1.60	0.90	2.03	1.6
G136	0.90	0.63	0.40	1.23	0.75625
G137	0.40	2.03	0.40	2.50	1.139063
G138	0.63	0.03	0.10	0.63	0.264063
G139	0.90	0.63	0.03	0.63	0.451563
G140	1.23	0.63	0.40	2.03	0.976563
G141	1.23	0.90	0.40	3.03	1.225
G142	0.40	2.03	0.40	2.50	1.139063
G144	0.90	0.90	0.10	0.63	0.564063
G145	0.40	0.63	0.10	0.63	0.4
G146	0.90	2.03	0.40	2.03	1.225
G147	2.50	0.90	0.40	2.03	1.314063
G148	0.40	2.03	0.40	0.90	0.826563
G150	2.50	0.63	0.40	1.23	1.05625

G151	0.63	0.63	0.40	0.90	0.625
G153	0.63	0.63	0.10	0.40	0.4
G154	1.60	0.90	0.40	0.63	0.826563
G155	0.63	0.23	0.10	0.63	0.351563
G156	2.03	0.63	0.90	2.50	1.40625
G158	2.50	0.63	0.63	0.63	0.976563
G159	0.90	0.23	0.10	0.10	0.264063
G160	0.40	0.23	0.00	0.03	0.1
G161	1.23	0.63	0.40	0.63	0.689063
G162	2.50	1.60	0.90	2.50	1.80625
G163	1.60	1.23	0.40	0.40	0.826563
G164	0.63	0.40	0.10	0.90	0.451563
G166	0.63	0.63	0.03	0.63	0.4
G167	0.40	0.40	0.90	2.50	0.9
G168	0.90	0.63	0.10	0.40	0.451563
G169	0.40	0.23	0.00	0.10	0.126563
G170	1.60	0.63	0.40	2.50	1.139063
G171	2.50	0.63	0.03	0.63	0.689063
G172	1.60	2.03	0.40	2.50	1.501563
G174	0.63	0.23	0.63	0.63	0.50625
G176	1.60	0.63	0.23	0.23	0.564063
G177	0.00	0.23	0.00	0.00	0.014063
G178	0.40	0.63	0.23	0.23	0.351563
G179	0.23	0.63	0.23	0.03	0.225
G180	0.23	0.23	0.03	0.03	0.1
Average	0.58	0.68	0.44	0.96	

Supplementary table 4. Mean performance of bread wheat genotypes for yellow rust severity traits across environments in Ethiopia, M=mean, SD=standard deviation, G=genotypes, N=number of environments/locations YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity, HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSsS= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GYPP=grain yield per plot

Level of G	N	HD	FD	MD	LA	PH	SL	TKW	NSsS	NKS
		M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD
G1	3	74.17±23.82	87.67±21.94	143.17±29.11	36.19±6.65	80.89±8.7	9.75±0.08	24.83±15.99	17.78±0.77	2.43±1.09
G2	3	69.67±27.28	87±22.52	144.33±32.15	40.81±16.49	90.44±4	9.14±0.17	31.24±20.11	18.05±0.48	2.78±1.07
G3	3	69.17±24.82	86.83±17.9	143.33±30.72	44.24±8.36	90.44±9.2	8.99±1.21	39.52±25.44	17.17±1.17	2.91±0.16
G4	3	74.5±22.49	86.83±21.36	143.83±26.73	32.23±7	82.5±8.93	9.37±0.42	36.05±23.2	17.78±0.54	2.29±0.73
G5	3	68.67±21.51	86.5±14.72	141.33±27.47	35.66±9.2	83.06±8.43	9.42±1.04	29.37±18.91	16.83±1.26	2.75±0.23
G6	3	68.17±22.33	85±16.45	139±28.01	32.29±3.5	89.11±10.93	9.42±0.46	32.04±20.63	18.17±1.32	2.43±0.52
G7	3	74.17±21.08	90.17±18.48	143.67±27.43	35.49±9.35	79.89±9.56	9.31±0.59	28.84±18.56	18±0.6	2.35±1.83
G8	3	69.83±22.67	86±19.92	141.33±27.08	26.59±2.22	85.89±8.94	8.89±0.68	22.34±14.38	17±1.33	2.44±1.03
G10	3	72±29.61	92.83±21.36	140.83±34.62	33.79±14.35	84.67±10.49	8.8±1.78	27.1±17.45	17.5±1.09	2.23±0.49
G11	3	71.17±24.7	86±19.05	140.83±30.37	40.4±15.86	80.22±4.98	8.47±0.54	26.34±16.96	16.72±0.92	2.79±0.83
G12	3	66.67±26.5	85.33±20.5	139.5±31.61	29.9±4.44	83.28±8.95	9.39±1.21	32.57±20.97	17.72±0.63	2.94±1.28
G13	3	71±24.52	86.17±16.74	145±29.82	32.75±9.45	83.89±13.75	9.92±1.23	33.46±21.54	18.5±1.09	2.27±0.76
G14	3	72.5±19.37	89.67±15.01	143.5±26.56	31.34±5.03	87.78±8.9	9.42±0.36	32.22±20.74	18.67±1.17	2.66±0.34
G15	3	72.83±21.2	90.17±16.74	143±27.14	30.22±10.32	83.67±9.29	9.39±0.75	29.9±19.25	17.5±0.93	3.09±1.09
G16	3	64.17±33.75	86.33±21.36	137.5±38.75	38.95±9.18	83.5±5.81	9.06±0.17	28.12±18.11	18.28±0.54	2.57±0.81
G17	3	70.17±25.04	89.17±17.61	144±30.79	33.63±10.83	83.39±7.5	8.97±1.38	28.84±18.56	22.28±5.68	3.08±1.1

G18	3	68.5±26.5	88.33±17.03	141±31.93	30.69±9.48	88.44±10.74	9.03±1.04	30.17±19.43	17.89±1.62	2.45±1
G19	3	72.83±25.17	92±19.05	142.83±31.56	35.04±11.85	89.61±7.93	9.14±0.64	30.44±19.6	19.28±1.93	2.72±1.05
G20	3	71.17±22.05	87.5±19.05	145.5±26.73	31.56±8.31	80.94±5.26	8.72±0.39	26.88±17.31	17.94±0.96	2.28±1.3
G21	3	68.83±29	90.33±18.76	143.17±34.49	42.44±20.62	87.94±11.51	10.75±1.09	39.16±25.21	17.39±1.25	2.78±1.07
G22	3	76.17±15.49	88.5±16.45	149±21.25	29.4±8.05	84.39±7.03	8.83±1	31.77±20.45	17.61±0.79	2.82±1.34
G23	3	73.33±21.81	92.17±15.88	148.5±26.75	40.51±17.01	88.94±6.22	10.22±1	40.41±26.01	19.61±0.54	3.41±1.11
G24	3	64±22.95	84.33±11.84	143.5±29.2	30.85±10.27	83.78±8.75	8.81±0.96	33.02±21.26	18.28±1.55	2.84±1.47
G25	3	75±23.66	89.83±21.36	143.67±29.11	28.44±7.08	80.78±5.3	8.78±0.48	34.62±22.29	18.61±0.42	2.39±1.25
G26	3	74.83±26.27	89.5±24.25	141.83±31.31	39.63±16.82	89.61±6.59	8.75±0.74	25.9±16.67	16.83±1.17	2.88±1.03
G27	3	72.17±25.81	87±21.65	143.83±30.82	31.61±11.4	83.11±6.15	8.28±0.42	30.26±19.48	18.11±0.26	2.5±1.17
G28	3	69.5±23.4	89.17±19.34	144.5±29.06	38.82±17.13	87.45±2.98	14.03±8.23	19.76±12.72	19.28±1.7	2.74±1.09
G29	3	75.17±22.14	89.67±20.21	143.33±27.6	25.87±4.17	83.22±8.61	8.97±0.49	30.17±19.43	17.44±0.51	1.99±0.91
G30	3	73±22.7	87.5±20.78	143.17±28.16	31.14±4.46	81.89±8.93	9.28±0.63	29.73±19.14	17.39±0.35	1.94±0.42
G31	3	74±24.39	87.5±22.52	141.17±30.15	35.93±9.19	83.28±11.58	8.82±1.17	26.17±16.84	17.39±0.79	2.59±1.12
G32	3	69.33±23.3	86.5±19.92	142.67±28.86	36.99±9.51	85.39±8.58	9.22±0.26	33.91±21.83	17.89±0.84	2.33±0.59
G33	3	71.83±22.53	90.67±15.88	143.67±28.51	29.35±9.92	93.22±9.14	9.89±0.7	32.66±21.03	18.55±1.93	2.65±0.59
G34	3	68.17±25.64	86±20.78	142.33±30.67	39.74±18.91	92.67±10.75	9.39±0.98	36.94±23.78	17.94±0.1	2.57±1
G35	3	71±25.7	87.67±21.07	141.83±31.2	40.62±11.86	90.61±6.97	9.61±0.82	31.6±20.34	17.55±0.69	2.4±0.57
G36	3	72.67±22.05	90±19.05	144.67±28.36	34.26±6.48	85.61±10.72	9.33±0.44	31.15±20.05	22.39±5.16	2.19±1.06
G37	3	72±25.24	88.17±21.94	144±30.51	31.82±6.04	84.61±9.95	9.63±1.22	27.23±17.53	18.11±0.51	2.5±1.1
G38	3	72.67±26.97	87.83±23.09	142.67±32.24	40.48±22.05	85.83±7.22	8.92±0.75	34.44±22.17	18.56±0.2	2.89±0.7
G39	3	71±25.7	92.67±21.07	143±30.77	34.44±10.97	89.11±7.3	9.15±0.94	36.67±23.61	18.67±0.34	2.79±0.82
G40	3	73.5±24.02	87.67±21.94	143.17±30.07	36.29±12.97	85.95±6.42	9.33±1.09	28.21±18.16	16.67±1.42	2.31±0.71
G41	3	70.33±23.62	85.67±19.34	140.33±29.27	33.89±7.92	84.5±8.13	53.44±76.26	30.88±19.88	18.5±1.92	3.06±1.35
G42	3	74.33±23.16	90.17±20.21	144±28.58	33.69±9	81.83±7.93	9.53±0.79	30.26±19.48	18.22±0.19	3.29±1.52
G43	3	75.17±25.17	91.5±21.65	144.5±31.58	33.65±12.27	91.16±16.13	9.33±0.73	33.11±21.32	18.66±2.08	2.65±0.59

G44	3	73.33±26.86	89±24.25	143.83±32.7	32.61±8.8	89±5.51	9.45±0.25	32.31±20.8	18.95±0.95	2.71±1.27
G45	3	69.67±27.44	86.83±22.23	140.5±32.94	37.18±9.54	95.72±5.23	9.32±0.63	34.27±22.06	17.11±0.92	2.77±0.78
G46	3	72.5±24.75	86.5±21.65	142.67±29.75	34.77±11.77	91.83±6.19	9.89±1.08	33.38±21.48	18.72±3.54	2.67±1.19
G47	3	71.83±25.31	88.33±22.23	143.83±30.18	28.2±8.98	92.11±4.82	8.8±0.84	35.16±22.63	16.55±0.25	2.22±1.51
G48	3	72.83±27.22	91.33±22.23	142.5±32.8	30.83±4.93	85.11±12.9	9.28±0.63	22.96±14.78	17.78±1.11	2.88±0.52
G49	3	73.5±25.7	90.67±21.07	143.17±30.72	35.84±4.38	82.95±13.35	9.42±0.51	28.39±18.28	17.39±1.39	2.64±0.92
G50	3	70.67±24.01	88.17±20.21	142.67±29.96	35.72±14.16	91.78±4.55	10.14±0.77	36.85±23.72	19±1.37	3.39±0.91
G51	3	71.83±24.48	88.33±21.36	126.73±48.45	34.09±9.11	87.83±3.92	8.58±0.68	34.18±22	18.17±0.44	2.93±1.57
G52	3	73.83±23.99	90.17±21.07	145.5±29.19	33.93±9.33	87.83±11.17	8.8±0.89	25.99±16.73	18.56±0.42	2.45±0.39
G53	3	71±26.02	88±21.65	140.83±32.04	39.59±13.97	90±10.53	9.47±0.38	33.11±21.32	17.94±0.59	2.84±0.93
G54	3	72.17±25.2	90.67±19.34	141.83±31.56	40.1±12.67	86.28±7.61	9.21±0.51	32.49±20.91	18.94±1.02	2.78±0.85
G55	3	67.83±23.38	85.17±17.61	142±29.19	35.08±11.08	88.44±7.19	9.28±0.42	31.51±20.28	18.56±1.83	2.75±1.63
G56	3	72.67±24.68	88.83±21.36	141±29.82	31.8±10.49	87.94±11.04	9.27±0.64	26.88±17.31	17.94±1.09	2.37±0.82
G57	3	71.5±24.62	87.17±21.94	144±30.15	34.09±3.75	90.17±5.43	9.11±0.42	38.45±24.75	18.17±0.76	2.53±0.55
G58	3	67.5±27.83	86.5±19.92	142.83±32.84	32.84±11.14	88.72±8.33	9.27±1.22	32.93±21.2	17.78±1.23	2.51±0.43
G59	3	69±22.29	87.17±15.88	143±28.46	42.32±17.66	88.67±7.89	9.22±0.19	37.29±24.01	17.61±0.63	3.05±0.6
G60	3	71.67±25.32	89.17±20.21	142.17±30.73	36.21±10.86	90.67±8.2	9.14±1.9	30.71±19.76	18.06±1.2	2.81±1.46
G61	3	71±22.57	90±16.45	143.83±29.2	33.89±8.24	89.45±9.51	9.11±0.63	29.82±19.19	18.22±0.54	2.16±0.89
G62	3	70.5±23.58	87.17±20.21	143.33±28.53	34.52±17.02	89.06±7.12	9.08±0.94	35.69±22.97	17.89±0.67	2.63±1.19
G63	3	73.5±24.84	93±18.19	145.5±30.28	39.32±10.09	82.39±11.59	9.75±1.5	26.7±17.19	19.22±1.17	2.5±0.44
G64	3	70.83±23.46	87.33±19.63	144.17±29.48	36.57±5.89	82.28±6.64	10.06±0.88	33.02±21.26	17.83±1.76	2.69±1.16
G65	3	72.33±24.13	89.5±20.78	143±29.79	36.66±11.19	84.94±5.14	9.11±0.52	28.93±18.62	18.39±0.79	2.6±0.93
G66	3	70.67±24.83	89±19.92	145.5±29.61	38.58±14.37	87.55±5.69	8.58±0.71	31.68±20.4	17.67±1.69	3.2±1.2
G67	3	71.17±23.61	89.67±17.61	144.67±29.7	39.35±13.56	84.5±7.34	9.97±0.59	34.89±22.46	17.72±1.45	3.73±0.78
G68	3	69.5±23.57	86.5±19.05	142.83±29.27	37.85±8.26	88.22±5.93	8.94±0.49	31.8±23.65	17.17±0.44	2.86±1.05
G69	3	74±22.7	88.5±20.78	143.5±27.74	38.63±8.19	87.45±8.32	9.47±1.26	24.56±15.82	17.28±1.11	2.72±1.13

G70	3	67±23.64	85.83±17.9	141.67±28.68	32.42±7.53	92.06±13.53	8.83±0.17	32.49±20.91	18.11±0.96	1.93±0.77
G71	3	70.33±23.62	87.67±19.34	146.33±30.05	37.98±12.82	84.94±8.37	9.81±0.47	31.15±20.05	17.66±1.44	2.61±0.25
G72	3	69.33±25.79	84.5±22.52	142.67±30.73	40.34±12.95	92.45±5.92	9.96±1	34.62±22.29	17.17±0.76	3.13±0.81
G73	3	71.67±23.03	88.33±19.63	143.33±28.04	32.51±14.12	86.28±10.71	9.08±0.84	31.51±20.28	17.06±1.46	2.5±0.6
G74	3	70±23.58	85.67±20.21	144.83±29.67	35.78±15.27	89.22±7.44	9.08±0.47	37.29±24.01	18.05±1.18	2.84±1.09
G75	3	73.83±23.38	89.17±21.07	143.33±30.17	33.45±9.06	85.78±12.19	9±0.47	29.82±19.19	17.94±1	3.23±1
G76	3	70.17±23.46	86.33±21.36	143.83±28.92	33.51±14.26	90.34±8.5	9.08±0.85	33.02±21.26	17.72±1.21	2.91±1.34
G77	3	73.5±22.12	89.67±19.34	144.5±27.88	31.43±6.67	84.72±11.12	8.72±0.17	25.81±16.62	18±1.64	2.53±1.71
G78	3	70.33±22.99	87.5±18.19	144.5±28.71	38.91±14.15	90.06±9.54	9.38±1.02	29.19±18.79	18.61±0.35	3.36±0.6
G79	3	73.5±25.53	90.33±21.36	143.67±30.73	36.95±12.21	93.11±1.36	8.98±0.47	30.08±19.36	17.11±0.96	2.64±0.71
G80	3	68.67±25.9	87.17±19.34	143.83±31.69	32.64±5.75	87.72±9.75	9.33±0.45	33.11±21.32	17.67±1.67	2.8±0.81
G81	3	69.17±28.98	87.67±21.94	142.33±34.26	40.12±16.56	88.61±6.8	9.61±0.48	33.91±21.83	17.61±2.26	3.12±0.5
G82	3	72.5±21.78	89.17±17.61	142.83±27.71	255.13±386.41	90.33±2.62	9.33±0.76	31.15±20.05	19.05±1.11	2.96±1.26
G83	3	69±25.43	82.17±19.34	143.67±31.07	47.99±36.58	84.55±12.07	9.03±0.68	33.29±21.43	17.89±0.96	10.78±13.21
G84	3	72.17±22.02	86.83±20.5	144±26.91	38.88±13	77.89±14.46	9.19±1.69	33.38±21.48	17.56±0.92	3.12±0.82
G85	3	74±23.79	88.67±21.07	143.5±31.24	36.94±10.76	90.44±10.89	9.55±0.98	38.09±24.52	16.83±0.6	10.54±13.35
G86	3	71.33±23.06	86.17±21.94	143.17±27.9	39.72±18.66	90.22±8.99	8.95±0.95	35.33±22.75	17.05±0.75	3.34±0.35
G87	3	73.33±21.66	90±18.19	142.5±28.08	31.65±5.53	86.94±9.99	9.69±1.19	26.79±17.24	17.34±1.26	2.63±0.39
G88	3	68.67±21.08	84.67±18.48	144.5±26.42	35.99±16.61	88.72±5.71	9.49±1.46	37.83±24.35	18.06±0.34	2.92±0.79
G89	3	72.5±26.68	89.5±21.65	144.5±31.75	31.32±9.32	89.11±6.75	9.27±1.11	32.75±21.08	17.22±3.35	11.18±13.03
G90	3	71.33±22.81	87.17±18.48	144.5±27.99	34.55±11.07	87.28±5.3	8.69±0.27	36.49±23.49	18.22±0.82	3.36±0.38
G91	3	73.83±24.77	90±20.78	144.67±30.55	33.12±10.13	85.84±5.06	8.75±0.47	32.66±21.03	17.94±0.68	2.35±0.57
G92	3	71.5±25.72	87.83±22.23	143.83±31.56	31.86±10.26	87.39±3.72	9.53±1	35.96±23.15	18.39±1.99	2.41±1.22
G93	3	72.83±21.7	89.17±19.34	144.5±27.14	38.13±12.34	89.78±7.53	9.03±0.59	35.51±22.86	17.33±1.53	2.62±0.41
G94	3	68.33±25.03	88.5±17.32	144.5±30.61	41.14±12.53	92.78±5.66	10.64±1.4	34.62±22.29	17.89±1.29	3.93±1.1
G96	3	68.83±28.06	87.67±21.94	140.17±33.33	38.57±11.28	92.78±4.11	9.95±1.6	33.06±21.29	17.22±0.54	2.49±0.95

G97	3	69.17±22.86	86.33±18.76	142.83±28.04	35.6±8.12	91.28±1.93	9.66±1.17	34.35±22.12	17.94±0.34	2.97±0.67
G98	3	70±26.42	88.5±19.92	142.5±32.31	39.51±6.8	90.5±8.29	9.47±0.46	36.05±23.2	18.06±1.78	2.77±0.84
G99	3	69.67±31.76	86.33±27.42	143.33±35.99	36.06±13.19	90.28±6.97	9.35±0.99	35.69±22.97	16.61±0.59	2.74±1.08
G100	3	71±26.02	88.5±21.65	143.33±31.34	36.31±5.56	83.22±12.21	9.46±1.33	29.1±18.74	16.89±1.17	2.49±0.63
G101	3	67.5±25.73	85±19.92	139.67±31.41	35.1±7.96	88.05±9.13	9.55±0.99	32.31±20.8	18.72±0.67	3.19±0.56
G102	3	71.83±27.4	88.33±23.09	141.33±32.66	27.87±6.77	85.55±8.9	9.12±1.35	33.11±21.32	16.11±1.42	2.18±0.84
G103	3	65.17±27.89	84.33±20.5	139.67±33.5	37.73±7.74	92.06±5.68	9.66±0.63	30.79±19.83	17.83±0.93	2.71±0.27
G104	3	71.83±22.32	89±18.19	145.33±27.74	37.43±16.83	88.11±5.25	9.31±0.9	33.55±21.6	18.67±1.17	3.18±1.32
G105	3	70.5±24.64	88.67±18.48	142.83±31.09	34.26±9.75	84.39±8.55	9.49±0.87	25.9±16.67	17.33±0.88	3±0.88
G106	3	76.5±24.14	93±21.65	146.83±28.86	39.39±14.55	87.39±9.69	9.97±1.34	25.9±16.67	18.11±0.1	2.78±0.51
G107	3	63±27.06	83±19.05	141±32.19	38.53±16.9	94.22±3.42	9.06±0.59	35.24±22.69	18.78±1.54	2.36±1.11
G108	3	68.83±23.09	86.83±17.03	140.83±29.14	39.39±8.24	87.33±9.1	8.94±1	34.53±22.23	18.22±0.86	2.75±0.52
G109	3	75.83±24.21	90.17±23.67	144.83±29.5	32.49±12.08	89.39±8.62	9.5±0.76	23.23±14.95	16.44±0.79	2.57±1.25
G110	3	77.5±24.5	93.33±22.23	146.67±29.7	35.84±15.85	90.28±6.4	9.6±0.44	28.84±18.56	17.33±0.73	2.73±1.12
G111	3	70.5±23.75	88.33±18.76	143.83±29.62	32.69±15.94	83.28±5.83	9.42±0.68	29.9±19.25	18.11±2.11	3.26±0.93
G112	3	69.5±24.71	85.83±20.5	145.17±29.73	47.52±17.77	86.72±1.51	9.75±0.96	30.08±19.36	18.5±1.16	2.74±1.32
G113	3	71.17±21.43	87.17±16.74	144.67±26.97	40.64±12	87.06±4.43	9.42±0.65	35.51±22.86	17.22±1.07	3.01±0.34
G114	3	68±22.25	88.17±15.01	143.17±28.92	39.6±11.23	83.95±7.42	8.95±0.75	30.35±19.54	18±0.72	2.88±0.52
G115	3	74.17±23.62	88.5±22.52	141.83±29.11	32.39±10.77	82.61±10.45	9.59±0.38	29.73±19.14	17.28±1.34	3.13±0.75
G116	3	71.83±26.08	89.17±21.94	143.67±31.87	41.51±14.52	92.17±10.17	10.08±1.09	33.38±21.48	18.11±1.34	2.74±0.12
G117	3	73±26.36	90.33±22.23	144.83±31.31	35.53±14.14	89.5±6.22	9.2±0.18	32.66±21.03	17.17±0.76	2.76±0.67
G118	3	67.83±26.8	86.83±18.76	141.33±32.47	41.43±14.81	87.39±1.11	9.19±1.27	34±21.89	18.17±2.35	2.66±1.16
G119	3	70.5±30.45	90±24.25	142±35.17	31.18±14.41	82.89±6.53	9.44±0.42	32.4±20.86	16.89±1.34	3.26±0.65
G120	3	74.17±26.7	90.67±23.67	143.83±33	37.56±17.72	84.83±3.12	9.39±0.59	35.42±22.8	16.61±0.42	2.4±0.47
G121	3	73.17±27.32	90.67±23.67	141.83±33.55	36.61±11.94	88.94±5.32	9.64±0.86	28.21±18.16	19.11±0.19	1.98±0.91
G122	3	70.83±24.77	87±20.78	146.33±24.76	38.92±13.01	89.17±5.07	9.81±0.93	33.64±21.66	17.89±0.42	3.05±1.13

G123	3	70.5±21.29	86.67±18.48	147.67±24.62	34.61±15.41	89.11±9.33	9.92±0.85	32.4±20.86	18.67±0.73	2.18±0.25
G124	3	68.33±25.77	87.17±20.21	143.5±31.1	36.35±14.31	88.17±11.84	8.71±0.51	36.31±23.38	17.11±1.07	2.74±1.64
G125	3	72.17±24.34	89.33±19.63	144.33±30.9	38.88±12.94	81.45±5.53	8.94±1.2	32.22±20.74	18.11±0.48	3.01±1.14
G126	3	73.83±25.23	87.83±23.96	142.33±30.24	31.87±6.12	81±6.23	9.25±0.13	22.61±14.55	18.17±0.44	2.28±0.35
G127	3	71.67±24.79	84.5±24.25	142.5±29.58	32.81±12.33	84.94±8.17	8.78±0.84	31.51±20.28	15.94±1.13	2.59±1.12
G128	3	69.17±23.19	89.17±19.34	143.33±28.37	30.67±8.32	90.11±7.49	8.78±0.79	26.17±16.84	17.11±0.38	3.28±0.74
G129	3	68.17±24.02	85.5±19.05	142.5±29.01	35.41±15.4	91.5±7.7	9.64±0.9	38.27±24.64	17±1.42	3.93±0.35
G130	3	70.67±23.68	86.83±19.63	144±29.19	38.27±12.62	91.44±6.97	9.08±0.75	30.65±22.7	17.44±0.92	2.87±0.8
G131	3	69.5±26.34	89±19.05	141.5±32.11	35.35±15.84	90.83±8.09	9.31±0.77	37.65±24.24	18.17±0.84	2.97±1.18
G132	3	69.17±25.15	85.83±20.5	142.5±30.28	38.65±15.05	89.67±7.15	9.83±0.43	36.31±23.38	18.05±1.18	2.69±0.31
G133	3	70.83±23.3	87.5±19.92	142.67±28.86	40.99±15.31	90.22±3.92	8.86±0.24	36.4±23.44	17.94±0.54	2.71±0.83
G134	3	66.5±26.63	85.83±19.63	141.67±31.88	27.67±10.27	81.78±5.34	8.92±0.66	32.4±20.86	17.33±0.44	3.41±0.78
G135	3	67.33±25.96	85.5±19.92	141.33±31.03	32.67±9.84	87.39±8.67	8.93±0.96	36.67±23.61	17.17±1.3	2.81±0.46
G136	3	72.17±24.99	89±20.78	142.83±31.09	30.78±10.55	90.28±6.88	9.39±0.82	30.62±19.71	17.78±0.54	3.43±0.49
G137	3	75±25.99	90.17±24.54	143.33±30.83	34±10.9	86.95±5.95	8.5±0.9	29.9±19.25	18.05±0.48	2.94±0.25
G138	3	73.17±28.44	90.83±23.96	142.17±34.15	35.13±9.36	89.94±7.51	9.6±0.94	31.68±20.4	18.28±0.39	2.59±0.98
G139	3	70.17±27.19	86.33±23.96	142.67±32.71	37.92±16.26	90.95±7.17	9.04±1.19	35.69±22.97	16.72±0.92	2.86±1.21
G140	3	73.5±24.86	88.67±22.81	143.33±30.52	36.44±9.34	86.05±9.96	9.33±0.44	31.95±20.57	17.61±0.68	2.27±0.95
G141	3	71.33±25.93	88.33±22.23	142.5±31.13	40.7±13.78	90.78±7.07	9.75±0.68	32.04±20.63	18.5±0.83	2.81±0.97
G142	3	72.17±26.15	88.83±22.23	145.5±31.71	30.48±9.3	87.5±10.13	9.89±0.71	23.05±14.84	18.17±2.08	3.02±0.86
G143	3	69.33±26.08	87.17±21.94	140.67±30.89	30.44±3.95	89.83±7.49	9.19±0.83	23.5±15.13	16.66±1.44	2.6±1.29
G144	3	71±23.24	87.33±19.63	143.33±29.29	42.82±18.46	90.89±8.01	9.5±0.43	35.2±22.66	18.05±1.6	2.9±0.98
G145	3	70.67±24.68	86.83±21.36	143.67±29.96	31.29±10.38	88.5±9.24	9.42±0.58	36.58±23.55	17.5±1.59	3.05±0.54
G146	3	71.33±22.67	86.5±19.92	143.67±28.02	35.69±14.67	89.5±6.66	9.97±0.78	35.69±22.97	18.61±1.07	2.79±0.83
G147	3	67.67±26.1	87.5±19.05	141.33±31.48	37.83±10.92	91.28±5.45	8.94±1.93	32.13±20.68	18.33±0.88	2.77±0.84
G148	3	68.83±23.18	85.83±17.9	141.17±28.59	33.09±13.69	89.67±6.93	9.44±0.95	29.55±19.02	17.28±1.23	2.91±0.16

G149	3	69.67±26.6	89.67±19.34	139.67±32.38	38.76±7.7	94.33±3.25	9.61±1.71	30.88±19.88	19±0.76	2.83±0.73
G150	3	67.33±27.45	86±20.78	141.33±32.42	32.2±7.09	94.11±2.43	9.58±0.9	35.96±23.15	16.55±0.95	2.43±1.7
G151	3	67.5±26.42	85.5±19.92	141±31.61	32.97±6.64	93.44±5.09	9.68±2.64	36.22±23.32	17.56±0.96	3.82±0.17
G152	3	70.83±24.37	90±18.19	143±30.39	38.17±4.85	91.39±9.72	9.55±0.25	29.46±18.96	17.78±1.58	2.46±1
G153	3	68±21.96	85.5±17.32	145.17±27.28	42.22±3.86	90.72±5.96	10±0.33	38.8±24.98	17.44±0.59	2.26±0.97
G154	3	70±24.88	87.17±20.21	142±30.12	35.17±12.64	85±9.54	8.92±0.92	29.01±18.68	17.78±0.25	2.7±0.62
G155	3	70.17±24.02	87±19.05	144.5±29.3	30.71±4.63	92.5±6.87	9.56±0.68	35.2±22.66	16.61±0.63	2.4±0.81
G156	3	71.33±27.57	89.5±21.65	144.5±33.75	51.02±17.9	88.72±10.86	9.19±0.81	35.51±22.86	17.39±1.17	2.3±0.72
G157	3	70±26.7	87.17±22.81	145.33±31.13	36.5±6.84	88.17±11.44	8.5±0.88	31.68±20.4	17.72±0.68	3.05±0.93
G158	3	71.17±23.22	89±18.19	146±28.65	32.3±4.13	85.11±13.14	8.41±0.5	32.57±20.97	15.83±1.09	2.63±0.34
G159	3	72.33±25.42	89±20.78	144±32.36	42.01±5.2	96.94±5.58	9.21±0.92	36.22±23.32	17.06±0.34	2.4±0.24
G160	3	68.83±29.05	87.5±22.52	142.5±34.37	27.67±7.03	85.78±8.32	9.31±1.25	28.66±18.45	17.45±1.7	2.56±0.19
G161	3	70.5±28.65	89.17±22.81	143.33±34.55	36.31±11.42	88.33±8.52	9.68±1.17	31.95±20.57	18.55±0.69	2.53±1.05
G162	3	70.33±24.48	86.33±21.36	143.67±29.41	29.85±11.92	84.5±7.67	9.58±1.12	33.38±21.48	18.78±0.67	2.63±1.27
G163	3	72.33±22.67	88±19.92	142.83±28.73	37.84±11.34	85.56±5.39	9.3±1	29.82±19.19	17.33±1.45	2.55±1.18
G164	3	73.5±27.18	90.83±23.09	143.67±32.19	35.72±7.15	90.33±4.92	8.92±1.24	33.29±21.43	17.06±0.92	2.44±0.7
G165	3	71.5±25.53	89.33±21.36	144±30.31	38.14±10.88	91.78±8.67	9.22±0.19	35.42±22.8	17.16±1.04	2.23±0.5
G166	3	71.33±22.68	88.17±17.61	147±28.36	38.22±16.43	91±4.96	10.31±1.54	36.58±23.55	20.22±2.96	2.9±0.83
G167	3	74.33±27.57	95.5±21.65	147.17±33.02	37±12.47	89.78±6.27	9.33±1.17	31.24±20.11	18.72±1.21	2.99±0.59
G168	3	73.33±26.73	91.67±21.94	145±31.75	36.05±11.6	86.33±11.26	9.33±0.44	30.88±19.88	17.72±0.25	2.25±0.46
G169	3	70±26.54	87.5±20.78	144±33.07	36.33±12.84	93.22±10.08	9.33±0.34	30.17±19.43	17.83±0.6	2.42±1.21
G170	3	71.5±25.1	87.33±22.23	148.83±29.55	37.76±11.13	87.72±2.87	9.61±0.1	34.35±22.12	17.17±1.17	3.02±1.14
G171	3	71.83±26.96	90.83±20.5	145.33±33.11	40.83±24.11	89.94±3.42	10.58±1.17	34.62±22.29	18.67±2.25	2.33±0.67
G172	3	68.67±26.69	87.17±20.21	144.17±31.76	32.28±8.66	88.22±7.32	9.57±0.65	25.72±16.56	18.56±1.5	2.66±1.21
G173	3	70±29.21	89.17±21.94	143±34.1	35.04±14.13	93.89±1.39	9.53±0.72	29.1±18.74	17.83±0.44	2.89±0.19
G174	3	69.67±22.86	86.83±18.76	146.17±28.29	35.92±7.06	82.94±10.04	9.11±0.63	36.13±23.26	16.06±1	2.28±0.94

G175	3	72.33±25.47	90.83±19.63	144.5±30.94	45.07±27.04	82.22±12.03	8.87±0.98	30.08±19.36	17.89±0.7	2.48±0.33
G176	3	76.83±27.74	94.17±23.67	143.83±33.74	37.21±14.24	83±4.86	8.97±0.75	34.84±22.43	19.17±1.17	2.95±0.34
G177	3	69.83±26.9	87.5±21.65	140.5±32.91	37.23±10.93	79.22±1.07	9.78±1.21	34.62±22.29	18.17±0.93	2.53±0.72
G178	3	66.5±23.4	89.17±19.34	146.17±28.59	34.67±11.08	89.61±8.58	9.11±1.14	37.74±24.29	18.33±0.34	2.72±0.93
G179	3	70.67±23.54	89.17±16.74	145.33±28.87	34.51±6.96	92±7.88	9.47±1.32	35.33±22.75	18.61±0.67	2.85±0.72
G180	3	72.17±24.61	91.5±18.19	145±31.28	37.43±6.91	90.28±6.27	9.83±1.26	32.04±20.63	18.5±0.76	2.91±0.69

Level of G	N	NKSs	SW	GY	YRPH	YRH	YRF	YRMM	YRM
		M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD
G1	3	2.65±1.35	1.51±0.88	24.83±15.99	8.67±7.37	16.67±12.22	19.67±13.05	23.33±15.53	26.33±16.76
G2	3	2.45±0.5	1.85±1	31.24±20.11	4.17±6.37	10.83±14.11	16.67±20.31	18.67±22.94	20.33±15.82
G3	3	3.02±0.42	1.9±1.13	39.52±25.44	1.67±2.89	9.5±8.53	20.33±18.77	22.5±20.32	26±25.81
G4	3	2.79±1.23	1.84±1.29	36.05±23.2	5.5±6.38	18±10.44	22.67±14.98	31.67±19.04	38.33±22.61
G5	3	2.8±0.46	1.57±0.49	29.37±18.91	14±5.29	30±5	34.33±5.13	41.17±8.75	44.67±23.71
G6	3	2.77±0.85	1.82±0.96	32.04±20.63	2.33±4.04	11.5±12.03	16.17±11.86	25.33±26.76	30.17±10.02
G7	3	1.9±1.33	1.51±1.01	28.84±18.56	15.67±14.01	19.33±18.88	37.5±20.46	46.17±20.89	51±30.03
G8	3	2.21±0.85	1.04±0.42	22.34±14.38	17±13.86	41±33.29	53.33±25.66	61.67±30.14	61.33±21.63
G10	3	2.79±1.26	1.66±0.94	27.1±17.45	7.5±7.5	15.33±15.01	1187±2042.1	16.67±17.56	19.5±33.84
G11	3	2.51±0.49	1.31±0.6	26.34±16.96	12.5±12.5	28.5±32.43	38.33±18.93	50±30.41	53.33±20.02
G12	3	2.6±0.85	1.55±0.93	32.57±20.97	15±15	36±31.19	46.67±27.54	54.33±28.75	57.67±31.75
G13	3	2.49±1.1	1.38±0.96	33.46±21.54	22.67±11.24	44.33±28.75	55.33±17.62	62±25.24	65±29.26
G14	3	2.72±0.26	1.74±0.87	32.22±20.74	5±3.61	10.17±8.25	12.83±9.12	17.67±14.57	20.5±22.91
G15	3	2.65±0.47	1.67±0.85	29.9±19.25	8.67±8.08	23.33±20.82	180.67±284.67	32±24.64	36.33±16.86
G16	3	2.57±1	1.63±0.86	28.12±18.11	11.67±10.41	25.5±24.25	26±23.52	29.33±28.75	32.67±25.7
G17	3	2.75±0.67	1.62±0.95	28.84±18.56	5.17±6.9	10.67±11.02	15.67±13.01	18.83±14.36	18.83±31.09

G18	3	2.4±0.99	2.07±0.43	30.17±19.43	7.5±9.01	20.83±22.68	23.5±24.07	29.83±31.09	32.83±14.36
G19	3	2.34±0.72	1.66±0.91	30.44±19.6	7.5±7.5	22.33±20.4	37±37.51	38.67±40.07	41±33.23
G20	3	2.39±1.5	1.32±0.86	26.88±17.31	16.67±14.43	32±23.07	43±30.61	46±30.61	50±42.58
G21	3	2.67±0.66	1.78±1.04	39.16±25.21	5.83±10.1	8±10.58	13±14.8	17.33±23.97	18±24.52
G22	3	2.37±0.53	1.37±0.69	31.77±20.45	17.33±15.04	30±25.98	43.67±33.47	49.67±36.61	60.33±23.43
G23	3	2.69±0.13	2.27±1.1	40.41±26.01	5±8.66	17.33±20.53	19.67±23.03	23±32.36	25.5±27.3
G24	3	2.56±1.33	1.55±1.09	33.02±21.26	21.67±18.93	40±35	46±37.99	53.67±41.96	55.33±31
G25	3	2.39±1.17	1.28±0.7	34.62±22.29	11±10.54	24.17±25.04	26.67±27.54	30.67±32.65	33.5±43.88
G26	3	2.71±0.99	1.62±0.72	25.9±16.67	5±8.66	22.5±19.84	26±22.54	28.67±25.79	33.33±32.55
G27	3	2.28±1.02	1.48±0.97	30.26±19.48	13.33±12.58	33.33±30.55	45.83±45.02	38.33±34.03	38.33±28.87
G28	3	2.68±1.07	1.95±1.12	19.76±12.72	0±0	8.83±7.69	14.67±11.06	15.67±11.68	22.67±34.03
G29	3	2.21±1.37	1.37±0.83	30.17±19.43	12.5±11.46	25.83±22.41	28.33±24.66	38.33±33.29	43.33±17.21
G30	3	2.33±1.04	1.52±0.83	29.73±19.14	12.5±15.61	30±27.84	36.67±35.12	41.67±42.52	45±37.86
G31	3	2.31±0.87	1.39±0.78	26.17±16.84	13.33±12.58	30±26.46	26.67±25.17	38.67±35.57	43.33±42.72
G32	3	2.6±1.02	1.58±0.95	33.91±21.83	0±0	13.33±12.58	12±10.58	24±28.16	25.83±37.86
G33	3	2.82±0.88	1.86±0.92	32.66±21.03	3.33±5.77	8.17±10.49	13±15.39	13±15.39	16.33±27.65
G34	3	2.46±0.93	2.36±1.5	36.94±23.78	1±1.73	8±8	16.67±15.28	17.67±18.56	24.33±20.98
G35	3	2.79±1.22	1.57±0.82	31.6±20.34	5±6.61	19.17±23.23	18.33±20.21	24.33±31.56	26.67±25.58
G36	3	2.24±1.05	1.62±0.94	31.15±20.05	11.67±10.41	25.83±22.41	36.67±35.12	38.33±37.53	39.17±30.55
G37	3	2.38±0.92	1.7±0.97	27.23±17.53	7.67±7.51	24.67±13.8	30.67±5.13	38.67±15.18	43.83±37.61
G38	3	2.83±0.51	1.81±0.94	34.44±22.17	1.67±2.89	11±12.12	11.67±13.2	14±17.06	14±20.1
G39	3	4.35±3.46	2.14±1.14	36.67±23.61	1.67±2.89	9±10.15	14.67±16.17	17±24.43	22.17±17.06
G40	3	2.59±1.26	1.31±0.71	28.21±18.16	9.67±9.5	26±10.15	33.33±12.58	39±12.17	44.83±25.48
G41	3	2.61±0.97	1.64±0.9	30.88±19.88	5±7	26±27.22	29.67±28.68	30.33±30.83	33.17±17.32
G42	3	2.79±1.09	1.54±0.83	30.26±19.48	5.33±5.03	13.33±12.58	24.33±22.9	24.33±22.9	28.33±29.78
G43	3	2.65±0.74	1.6±0.8	33.11±21.32	15.83±12.83	41.67±35.47	49±39.15	52±37.04	55.83±28.18

G44	3	2.71±1.19	1.79±1.03	32.31±20.8	13.33±10.41	27±10.58	45±31.22	39.33±17.21	41±35.03
G45	3	2.77±0.64	1.74±0.79	34.27±22.06	2.5±2.5	12.5±7.5	14±10.54	22.67±20.11	24.5±14.42
G46	3	2.56±1.01	1.48±0.72	33.38±21.48	8.33±10.41	18.33±16.07	22.33±19.4	31.67±28.43	36.67±19.58
G47	3	2.05±1.34	1.63±1.17	35.16±22.63	7.33±6.43	18.67±16.44	25±21.79	27.33±24.68	32.33±32.15
G48	3	2.61±0.26	1.87±0.83	22.96±14.78	11.67±10.41	22.5±9.01	48.33±28.43	50±26.46	53.33±28.22
G49	3	2.58±0.9	1.45±0.75	28.39±18.28	16.67±6.29	36.67±20.21	48.33±30.14	49.33±32.96	52.5±32.15
G50	3	3.17±0.76	3±2.01	36.85±23.72	17.5±20.46	25.33±22.37	27±18.36	40±34.51	42.83±30.31
G51	3	2.77±1.48	1.58±0.96	34.18±22	4.17±7.22	12.5±11.46	17.17±14.97	23.33±20.82	26.67±34.74
G52	3	2.95±0.63	1.31±0.3	25.99±16.73	26.67±15.28	47±29.61	57±32.05	66.67±17.56	68.33±23.63
G53	3	2.78±0.85	1.61±0.81	33.11±21.32	2.5±4.33	16±13.89	20.67±17.93	22±20.3	26.33±17.56
G54	3	2.66±0.61	1.76±0.99	32.49±20.91	1.67±2.89	15.33±14.57	20±18.33	22±21.07	24.33±22.81
G55	3	2.58±1.45	1.69±1.25	31.51±20.28	7.5±7.5	23.33±20.21	29.33±25.72	32.5±28.83	36.67±21.78
G56	3	2.43±0.88	1.33±0.7	26.88±17.31	11.67±5.77	19.67±5.69	22±11.53	32.67±20.98	32.67±32.15
G57	3	2.75±0.88	1.64±0.9	38.45±24.75	3±2.65	11.67±10.12	14.67±12.86	18±16.37	19.67±20.98
G58	3	2.67±0.72	1.72±0.79	32.93±21.2	5±8.66	8.33±9.24	10±12.12	17±25.12	18±14.98
G59	3	3.1±0.8	2.19±1.26	37.29±24.01	6±7.94	15.83±20.51	10.33±3.79	27.67±18.45	31.83±25.98
G60	3	2.58±1.21	1.72±1	30.71±19.76	9.17±1.44	13.83±8.61	23.67±11.5	29.33±14.01	33.33±14.63
G61	3	2.15±0.95	1.5±0.88	29.82±19.19	11.67±7.64	21±16.37	27.67±23.59	31±24.52	37±16.07
G62	3	2.46±0.76	1.46±0.7	35.69±22.97	15.83±11.81	38.33±10.41	41.67±10.41	43.33±15.28	45±27.87
G63	3	2.67±0.73	1.64±0.69	26.7±17.19	25±8.66	40±18.03	50±25.98	48.33±23.09	50±15
G64	3	2.3±0.78	1.46±0.76	33.02±21.26	15.67±6.03	45.67±24.01	50±26.46	60.33±17.9	59±21.79
G65	3	2.37±0.4	1.53±0.59	28.93±18.62	15.83±5.2	33.33±15.28	44.33±41.79	34.33±26.01	41.67±19.16
G66	3	2.76±0.71	1.82±0.89	31.68±20.4	6.17±5.84	23±20.66	29.33±23.8	33.67±28.92	34.67±20.21
G67	3	3.01±0.16	2.04±0.93	34.89±22.46	10±13.23	17.33±19.66	25.67±30.24	26.33±29.87	29.83±27.61
G68	3	2.81±1.07	1.7±0.94	31.8±23.65	7.5±2.5	15±0	22.33±8.74	29.33±13.65	32.5±35.43
G69	3	2.61±0.84	1.57±0.71	24.56±15.82	11.67±16.07	32.67±20.4	38.67±30.53	45±38.16	45±12.5

G70	3	1.88±0.65	1.49±0.92	32.49±20.91	8.33±7.64	22.67±20.53	18.67±16.65	34±32.6	35.33±38.16
G71	3	2.88±0.59	1.97±0.93	31.15±20.05	5±5	12.83±7.01	16.67±9.45	19±12.12	19.5±32.87
G72	3	2.85±0.47	1.72±0.76	34.62±22.29	7.67±13.28	19±21.28	21.67±20.21	29.33±31.72	32.67±12.28
G73	3	2.61±0.69	1.67±0.88	31.51±20.28	5.17±4.48	19.5±20.57	9.67±13.43	26.33±25.54	35.5±34.08
G74	3	2.72±0.78	1.65±0.9	37.29±24.01	0±0	8.5±6.73	14.33±9.07	17.33±9.71	17.33±13.7
G75	3	3.24±0.75	1.55±0.58	29.82±19.19	14.17±12.83	24.33±19.14	35.33±25.4	38±25.24	41.33±9.71
G76	3	2.47±0.92	1.63±1.01	33.02±21.26	12.5±7.5	27.67±21.94	34.33±9.81	48.33±21.03	49.33±28.11
G77	3	2.09±1.06	1.41±0.86	25.81±16.62	10±13.23	37±35.17	36.67±32.15	46.67±43.11	46.67±21.01
G78	3	3.41±0.64	2.15±0.75	29.19±18.79	2.5±4.33	16.67±17.56	19±16.82	22±22.52	26.67±43.11
G79	3	2.92±0.91	1.65±0.78	30.08±19.36	7.67±13.28	10.83±10.1	16.5±16.02	14.17±14	17±23.63
G80	3	2.58±0.55	1.53±0.83	33.11±21.32	6.33±5.51	18±17.52	17.33±20.53	29.33±25.42	31.67±12.77
G81	3	3.12±0.4	1.93±0.86	33.91±21.83	3±5.2	8.67±8.5	13.67±16.5	14.67±20.43	19.33±27.54
G82	3	2.85±1.17	1.53±0.88	31.15±20.05	5.33±5.03	13.33±12.22	12±10.58	23.67±23.5	26.67±20.55
G83	3	10.61±13.33	5.02±4.69	33.29±21.43	6.67±7.64	11±1.73	18.33±2.08	19.33±8.14	24±28.1
G84	3	2.73±0.33	1.64±1.01	33.38±21.48	16.67±14.43	31.67±27.54	23.33±25.17	42.67±34.44	56.67±4.58
G85	3	10.77±13.17	1.61±0.69	38.09±24.52	8.33±7.64	25±21.79	38.33±33.29	38.33±33.29	41.67±10.41
G86	3	3.68±0.5	1.91±0.72	35.33±22.75	4.17±5.2	13±12.53	12.67±12.06	17.33±20.53	18±36.17
G87	3	2.57±0.52	1.33±0.55	26.79±17.24	15±13.23	32±23.07	35±30.41	50.33±39.12	54.67±20.3
G88	3	2.92±0.79	1.8±0.93	37.83±24.35	1.67±2.89	10.33±13.05	4.67±5.03	17±20.66	19±40.25
G89	3	10.85±13.31	2.06±0.92	32.75±21.08	5±8.66	14.67±13.65	22±20.3	25±24.52	27.33±23.3
G90	3	3.36±0.33	1.71±0.64	36.49±23.49	0±0	7±7	15.33±16.04	18±20.3	24.5±24.99
G91	3	2.79±0.73	1.81±0.93	32.66±21.03	4.67±5.03	14±14	18.67±20.13	25±30.51	25.67±27.99
G92	3	2.69±1.29	1.81±1.29	35.96±23.15	4.67±4.51	14±16.37	17.33±20.53	24±31.75	26±30.24
G93	3	2.73±0.57	1.89±1.02	35.51±22.86	3±5.2	6±7.21	6±6	10.67±11.59	11±33.65
G94	3	3.43±0.9	2.09±0.96	34.62±22.29	3.67±6.35	17±15.39	22±20.3	31±30.05	31±11.53
G96	3	2.6±1	1.61±1.03	33.06±21.29	3±5.2	11.33±14.01	11±12.12	16.33±17.04	19±30.05

G97	3	3.19±0.42	1.66±0.78	34.35±22.12	3.33±5.77	14±17.78	11.58±12.02	23±30.05	25±14.8
G98	3	2.77±0.51	1.85±1.01	36.05±23.2	6.67±11.55	11±16.52	20±26.46	20.67±21.78	25±31.95
G99	3	2.8±1.15	1.66±0.97	35.69±22.97	13.33±12.58	27.5±25.37	41.17±37.14	37.17±25.91	37.17±26.29
G100	3	2.54±0.7	1.47±0.7	29.1±18.74	20±5	36.33±24.19	43.33±11.55	55±25	60±25.91
G101	3	2.86±0.56	1.8±0.75	32.31±20.8	12.5±12.5	26.33±26.08	40.67±36.83	51±31.43	51±27.84
G102	3	2.57±1.4	1.5±0.9	33.11±21.32	7.33±6.43	19.67±21.73	17.33±15.14	25.67±31.63	30±31.43
G103	3	2.88±0.43	1.6±0.73	30.79±19.83	15.17±10.25	19±19	23.33±23.44	27±28.62	27.67±27.4
G104	3	2.9±0.62	1.7±0.91	33.55±21.6	3.33±5.77	14.67±14.5	27.67±29.26	22.33±17.62	24±28.11
G105	3	2.84±0.44	1.45±0.61	25.9±16.67	11.67±10.41	25.33±17.47	31.67±10.41	41.67±20.21	45±17.52
G106	3	2.83±0.44	1.74±0.7	25.9±16.67	15±13.23	26±21.28	37.67±13.65	56.67±20.21	61.67±22.91
G107	3	2.42±1.23	1.6±1	35.24±22.69	6±10.39	14±13.53	19.17±20.05	19.5±20.57	22±16.07
G108	3	2.86±0.56	1.84±0.93	34.53±22.23	5±8.66	15.83±15.07	14.17±12.33	22.5±22.5	22.5±18.08
G109	3	2.4±1.1	1.3±0.66	23.23±14.95	18.33±2.89	35±5	43.33±7.64	50±8.66	55±22.5
G110	3	2.62±1.06	1.43±0.62	28.84±18.56	15.83±8.04	25±8.66	30±8.66	41.67±16.07	43.33±13.23
G111	3	2.59±0.23	1.68±0.62	29.9±19.25	11.67±5.77	26±3.61	38.33±10.41	44±11.53	45.33±15.28
G112	3	2.85±1.42	1.84±1.03	30.08±19.36	15±5	31.67±14.43	36±11.53	45.33±12.66	45.33±13.8
G113	3	3.01±0.45	1.75±0.61	35.51±22.86	14.17±1.44	31.67±10.41	38.33±20.21	45±27.84	49.33±12.66
G114	3	2.77±0.51	1.66±0.78	30.35±19.54	12.5±6.61	21.67±5.77	31.67±7.64	41.67±15.28	43.33±28.75
G115	3	2.96±0.23	1.59±0.52	29.73±19.14	17±5.2	35.33±8.39	46.67±11.59	50±13.08	53.33±17.56
G116	3	3.12±0.33	1.86±0.58	33.38±21.48	8.33±5.77	25.67±8.14	34±13.89	34±13.89	34±18.82
G117	3	3.04±0.33	1.79±0.65	32.66±21.03	10±10	23.33±11.55	30.33±22.37	37±27.87	38.67±13.89
G118	3	2.89±1.02	1.81±1.01	34±21.89	3.33±5.77	14.67±18.18	25.67±30.92	26.67±27.54	26.67±28.73
G119	3	3.04±0.55	1.59±0.65	32.4±20.86	15±0	34.17±5.2	42.5±15.61	49.17±22.41	50.83±27.54
G120	3	2.56±0.74	1.35±0.56	35.42±22.8	10±5	24.67±18.58	40.67±25.32	40.67±25.32	43.33±21.26
G121	3	2.44±0.68	1.53±0.98	28.21±18.16	6.67±7.64	16±12.49	27±12.12	30±13.23	31.33±24.66
G122	3	2.61±0.42	1.93±0.9	33.64±21.66	3±5.2	12.67±20.23	14±22.54	17.33±28.31	20.33±11.85

G123	3	2.52±0.74	1.68±0.85	32.4±20.86	3±5.2	23.33±12.34	23.33±7.57	32.33±19.66	32.33±33.5
G124	3	2.57±1.49	1.85±1.15	36.31±23.38	3.67±5.51	13.33±16.65	15.33±16.04	28±32.74	28.67±19.66
G125	3	2.79±0.62	1.92±0.96	32.22±20.74	2.5±2.5	6.17±7.15	6.67±8.33	13.33±15.95	15.83±32.52
G126	3	2.78±0.79	1.32±0.4	22.61±14.55	15±5	24±8.54	41.67±17.56	50±13.23	55±18.39
G127	3	2.54±1.04	1.59±1.1	31.51±20.28	16.67±7.64	29.17±9.46	40±8.66	41.67±11.55	43.33±10
G128	3	4.56±2.86	1.55±0.58	26.17±16.84	13.33±7.64	25±10	23.33±25.17	38.33±20.21	43.33±10.41
G129	3	3.54±0.47	2±0.77	38.27±24.64	10±8.66	26±21.28	36±33.51	36±33.51	40.17±18.93
G130	3	2.81±0.8	1.93±1.12	30.65±22.7	5±5	13.33±11.55	23.33±20.82	26.67±23.09	28.33±36.06
G131	3	2.48±0.21	1.81±0.83	37.65±24.24	7.33±8.74	14.5±13.26	21.83±18.51	23.17±18.39	26.5±24.66
G132	3	2.74±0.31	1.78±0.88	36.31±23.38	6.67±5.77	17±12.17	22.67±18.61	23±17.58	23±21.15
G133	3	2.6±0.64	1.85±1	36.4±23.44	1.33±2.31	8.5±9.04	12.17±12	17.83±18	17.83±17.58
G134	3	3.3±0.82	1.68±0.64	32.4±20.86	8.67±9.02	21±15	28.67±22.03	32±26	32.67±18
G135	3	2.76±0.29	1.8±0.83	36.67±23.61	3.33±5.77	17.5±20.46	19.17±20.05	22.5±25.37	25±26.03
G136	3	3.37±0.57	1.72±0.58	30.62±19.71	12.5±13.92	21.33±20.13	35.33±33.56	35.67±25.58	39.67±27.84
G137	3	2.88±0.48	1.81±0.67	29.9±19.25	1.67±2.89	13.67±18.72	15.67±21.36	26.33±38.08	26.33±28.38
G138	3	2.75±0.96	1.87±1.01	31.68±20.4	9.5±10.04	19.67±21.13	16.33±14.15	29.67±30.53	33±38.08
G139	3	2.53±0.88	1.6±0.81	35.69±22.97	6.67±5.77	15.83±14.22	14.17±13.77	29.17±27.65	29.17±30.81
G140	3	2.5±1.1	1.56±0.79	31.95±20.57	13.83±12.41	29±25.94	41.67±23.63	45.33±22.03	48.67±27.65
G141	3	2.86±1.04	1.65±0.81	32.04±20.63	8.83±9.57	24.17±21.69	17.17±14.78	33±22.27	39.83±24.91
G142	3	2.57±0.17	1.33±0.47	23.05±14.84	18.33±12.58	40.33±35.5	53.33±27.54	61.67±22.55	65±16.13
G143	3	2.15±0.69	1.07±0.39	23.5±15.13	17±15.72	35.67±24.01	36±16.37	48.67±29.67	60±25
G144	3	3.23±0.85	1.81±0.63	35.2±22.66	2.33±4.04	11.67±14.57	14.67±16.17	20.67±26.1	20.67±27.84
G145	3	3.16±0.45	1.75±0.92	36.58±23.55	5.83±5.2	17.5±15.61	35±31.22	41.67±38.19	45±26.1
G146	3	2.62±0.78	1.64±0.8	35.69±22.97	5.83±5.2	20±20	26.67±25.17	35±35	38.33±39.69
G147	3	2.83±0.29	1.97±0.93	32.13±20.68	5±8.66	13.5±15.22	10.17±10	15.17±17.96	15.17±37.53
G148	3	3.02±0.42	1.56±0.63	29.55±19.02	12.5±12.5	21.67±18.93	28.33±25.66	31.67±28.43	33.33±17.96

G149	3	2.61±0.51	1.79±0.88	30.88±19.88	5±5	16.67±15.28	26±23.52	30±26.06	32.67±29.3
G150	3	2.21±1.38	1.64±1.15	35.96±23.15	6.67±11.55	10.33±13.8	19±27.07	14.67±19.66	15.67±26.76
G151	3	3.48±0.42	1.85±0.68	36.22±23.32	3.33±5.77	12.5±15.61	14±15.1	19.33±23.16	21.67±19.14
G152	3	2.18±0.71	1.19±0.66	29.46±18.96	17±11.53	31±24.52	42±27.51	53.33±32.53	56.67±25.66
G153	3	2.31±0.8	1.69±1.05	38.8±24.98	5.67±7.37	18.5±23.54	17.5±20.46	25.83±34.49	25.83±33.29
G154	3	2.64±0.54	1.7±0.89	29.01±18.68	13.33±15.28	29.17±13.77	30.83±8.04	39.17±22.41	42.5±34.49
G155	3	2.62±0.74	1.78±1.01	35.2±22.66	10.17±9.22	28.33±27.54	29.33±22.94	41±34.39	45.33±24.11
G156	3	2.41±0.81	1.48±0.8	35.51±22.86	13.33±12.58	31.67±28.43	29.17±25.54	40±36.06	40±35.5
G157	3	2.88±0.77	1.71±0.79	31.68±20.4	12.5±12.5	33±30.61	41±38.51	45.33±39.5	50.5±36.06
G158	3	2.86±0.56	1.81±0.74	32.57±20.97	7±6.56	19.5±20.02	15±13.08	25.83±27.65	26.1±40.54
G159	3	2.74±0.68	1.62±0.63	36.22±23.32	3±3.61	12±10.44	9.67±10.6	17±14.93	19±27.61
G160	3	2.72±0.67	1.48±0.53	28.66±18.45	10±10	21.67±20.21	31.67±30.14	43.33±40.41	46.67±16.82
G161	3	2.64±1.04	1.57±0.82	31.95±20.57	3.33±5.77	10.17±11.73	14.83±16.13	19.83±21.1	21.5±45.09
G162	3	2.85±1.46	1.77±1.1	33.38±21.48	7.67±7.37	13.17±17.48	23±15.72	34±34.22	34.33±21.02
G163	3	2.44±1.1	1.45±0.81	29.82±19.19	5.17±5.25	20.67±20.03	17.33±18.04	33.67±30.66	38.33±33.86
G164	3	2.78±1.17	1.52±0.79	33.29±21.43	2.33±2.52	13.5±15.22	11.5±12.03	24±31.75	24.17±35.47
G165	3	2.56±1.01	1.54±0.94	35.42±22.8	5±5	21.67±18.93	37±32.05	38.67±30.01	42±31.66
G166	3	2.9±0.83	2.02±1.31	36.58±23.55	1.67±2.89	16±17.69	18.33±20.21	23.67±28.29	28±32.74
G167	3	2.87±0.28	1.58±0.64	31.24±20.11	6.67±7.64	21.67±20.21	16.33±14.15	26.67±25.17	26.67±33.42
G168	3	2.47±0.79	1.43±0.85	30.88±19.88	18.33±16.07	36.67±31.75	49.67±36.61	61±31.19	66±25.17
G169	3	2.47±1.29	1.69±1.05	30.17±19.43	6.67±7.64	13.33±12.58	19.33±16.02	30.5±18.66	36.33±29.55
G170	3	2.63±0.47	2.58±1.82	34.35±22.12	11.67±10.41	31.67±28.43	43.33±40.41	45±40.93	50±25.7
G171	3	2.77±1.39	2.08±1.47	34.62±22.29	1.67±2.89	5±5	19.33±25.32	20±26.46	23.33±44.44
G172	3	2.55±1.03	1.48±0.9	25.72±16.56	13.33±11.55	32.33±17.79	46.67±15.28	55±22.91	58.33±32.15
G173	3	2.83±0.44	1.88±0.69	29.1±18.74	8.33±7.64	17.5±15.61	26.67±25.17	31.67±30.14	35±25.66
G174	3	2.22±0.97	1.54±1.02	36.13±23.26	13.33±12.58	34.33±27.59	38±25.24	53±39.4	56.33±32.79

G175	3	2.47±0.47	1.43±0.58	30.08±19.36	16.67±15.28	32±24.64	42±37.04	45.33±37.22	48.67±42.19
G176	3	3.06±0.38	1.98±0.82	34.84±22.43	1.67±2.89	5±4.58	8±8	11±14.18	13±39.88
G177	3	2.45±0.53	1.92±1.13	34.62±22.29	7±7.55	17.67±17.5	20.67±20.03	30.67±35.8	32±16.09
G178	3	2.77±1.01	1.82±1.01	37.74±24.29	7.5±10.9	19±20.07	21.33±20.13	32.67±35.23	34.33±35.38
G179	3	2.9±0.81	1.86±0.87	35.33±22.75	2±2.65	13.67±18.72	17.33±20.53	29.67±39.88	31±35.02
G180	3	3.02±0.87	1.71±0.76	32.04±20.63	4.33±4.04	11.5±13.26	26.67±29.7	31.67±35.95	36.33±39.15

Supplementary table 5. Summary of individual marker-trait associations for yellow rust severity resistance. The table reports yellow rust severity traits, Allele ID, Chromosome, physical position, significance value (p. value a), additive effect, MAF= Minor allele frequency, SNP position, and "R2 " value = proportion of phenotypic variation explained by marker. YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity

Trait_Location	AlleleID	Chr	Position (bp)	P.value	maf	Nobs	Rsquare	Add effect	P.value (-log(p value))	Agro nomic Trait
YRF_Combined	1062638 F 0-63:G>A-63:G>A	1A	512496605	2.07E-10	0.064606742	178	10.52878803	13.67918118	9.683035703	YRPH
YRF_Combined	1080608 F 0-31:T>C-31:T>C	1A	588261371	3.93E-07	0.134831461	178	10.45977872	9.087577376	6.405480029	YRPH
YRF_Combined	3951391 F 0-7:A>C-7:A>C	2D	74936166	0.0004223	0.148876404	178	10.23841039	5.053503567	3.374360864	YRPH
YRF_Combined	4329688 F 0-33:A>T-33:A>T	2D	591603469	0.0007482	0.123595506	178	11.65423207	7.075524791	3.125974494	YRPH
YRF_Combined	985245 F 0-35:A>G-35:A>G	3B	20999249	0.0002558	0.162921348	178	10.43050449	6.222299404	3.592058294	YRPH
YRF_Combined	1393516 F 0-15:G>A-15:G>A	3D	569281482	3.38E-07	0.359550562	178	10.21138576	5.481496906	6.470545449	YRPH
YRF_Combined	7351530 F 0-11:G>A-11:G>A	5A	46483467	1.49E-08	0.036516854	178	10.03737672	17.62244701	7.826092227	YRPH

YRF_Combined	5582673 F 0-31:G>T-31:G>T	5A	81392307	2.64E-05	0.04494382	178	12.13322412	10.96260094	4.579088955	YRPH
YRF_Holeta	5371122 F 0-24:G>C-24:G>C	2A	733216778	0.0009722	0.176966292	178	10.73655457	5.903014958	3.012231191	YRPH
YRF_Holeta	2262895 F 0-38:G>C-38:G>C	2B	410189157	0.0003326	0.134831461	178	11.69047999	6.742483461	3.478018672	YRPH
YRF_Holeta	1073870 F 0-52:G>T-52:G>T	3A	250818410	0.0005852	0.188202247	178	10.58024823	4.74716349	3.232706417	YRPH
YRF_Holeta	1207429 F 0-60:A>T-60:A>T	3A	639713075	7.34E-05	0.129213483	178	10.34304369	6.91743551	4.134275628	YRPH
YRF_Holeta	1108433 F 0-35:C>T-35:C>T	5A	429474426	0.000425	0.148876404	178	10.56693589	5.254267981	3.371570716	YRPH
YRF_Holeta	1214898 F 0-48:C>A-48:C>A	7A	96563306	0.0009503	0.494382022	178	10.73655263	3.865577862	3.022160189	YRPH
YRF_Holeta	2246599 F 0-51:G>C-51:G>C	7D	14621383	0.0009121	0.47752809	178	10.74325263	3.413826607	3.039952912	YRPH
YRF_Kulumsa	1052695 F 0-41:C>G-41:C>G	1A	16417326	0.0006145	0.463483146	178	9.793453132	4.823149979	3.131628158	YRPH
YRF_Kulumsa	2294592 F 0-64:T>C-64:T>C	1B	73576935	0.0007385	0.04494382	178	9.374543979	10.21950464	3.102966919	YRPH
YRF_Kulumsa	4910323 F 0-27:C>A-27:C>A	1D	54339059	0.0002168	0.073033708	178	7.942642195	9.382725669	3.169061797	YRPH
YRF_Kulumsa	1062073 F 0-41:C>T-41:C>T	7A	44352216	0.0006775	0.483146067	178	9.155583547	4.919901417	3.133216287	YRPH
YRF_Meraro	1080608 F 0-31:T>C-31:T>C	1A	588261371	0.0007358	0.134831461	178	11.84245761	15.55487871	3.133216287	YRPH
YRF_Meraro	1000215 F 0-22:G>T-22:G>T	2A	772984442	1.84E-05	0.08988764	178	14.0536438	18.88761257	4.734662542	YRPH
YRF_Meraro	4910926 F 0-20:T>C-20:T>C	2B	768053989	0.0008273	0.087078652	178	11.74702582	16.91777174	3.082337768	YRPH
YRF_Meraro	2264044 F 0-68:T>C-68:T>C	3B	463461507	0.0004369	0.157303371	178	12.14656625	14.07897003	3.359607674	YRPH
YRF_Meraro	988248 F 0-62:C>A-62:C>A	4B	66799362	0.0008952	0.084269663	178	11.74703877	12.89377617	3.048091368	YRPH
YRF_Meraro	7351530 F 0-11:G>A-11:G>A	5A	46483467	3.96E-17	0.036516854	178	11.97277253	71.22509832	16.40210456	YRPH
YRF_Meraro	7351742 F 0-7:C>A-7:C>A	5D	515407161	3.10E-08	0.056179775	178	13.115192	33.839819	7.508153061	YRPH
YRF_Meraro	1103333 F 0-58:C>T-58:C>T	5D	529525683	0.0003831	0.115168539	178	11.55040731	17.57432625	3.416657679	YRPH
YRF_Meraro	1021513 F 0-60:G>A-60:G>A	5D	529525749	0.0001642	0.103932584	178	11.52816501	20.01023775	3.784707195	YRPH
YRF_Meraro	1150470 F 0-10:C>T-10:C>T	5D	533205336	0.000116	0.087078652	178	12.98406795	21.26052675	3.935433709	YRPH
YRF_Meraro	1019642 F 0-23:A>G-23:A>G	6B	291067106	0.0002489	0.280898876	178	12.52961221	9.937734095	3.60396925	YRPH

YRF_Meraro	4991969 F 0-16:T>C-16:T>C	6B	476032032	0.0002039	0.078651685	178	11.68025701	11.90237461	3.69066675	YRPH
YRF_Meraro	1034248 F 0-41:T>C-41:T>C	6B	583215607	0.0003307	0.078651685	178	11.83009597	20.96705118	3.480605843	YRPH
YRF_Meraro	1043873 F 0-67:C>T-67:C>T	7A	50346076	0.0009684	0.112359551	178	11.74702583	14.83318714	3.013928696	YRPH
YRF_Meraro	989752 F 0-42:G>A-42:G>A	7A	128909455	0.0008746	0.123595506	178	11.74702583	-13.4519184	3.058185374	YRPH
YRH_Combined	1002704 F 0-50:T>C-50:T>C	2B	243083729	0.0001925	0.193820225	178	10.52878803	4.111377197	3.715564959	YRH
YRH_Combined	2279027 F 0-66:G>T-66:G>T	2B	647897009	0.0003067	0.179775281	178	10.03737672	4.602258675	3.513252719	YRH
YRH_Holeta	3020463 F 0-7:A>G-7:A>G	1D	7734813	0.0006264	0.238764045	178	1.298824398	2.826469346	3.203136382	YRH
YRH_Holeta	2279027 F 0-66:G>T-66:G>T	2B	647897009	0.0004297	0.179775281	178	1.298824398	3.506483739	3.366838724	YRH
YRH_Holeta	1212106 F 0-13:T>C-13:T>C	2B	790748970	9.20E-05	0.137640449	178	1.298824398	5.041856397	4.036356111	YRH
YRH_Holeta	1393706 F 0-36:C>T-36:C>T	2B	793146869	0.000677	0.143258427	178	1.298824398	4.121882794	3.169431348	YRH
YRH_Holeta	999811 F 0-24:G>C-24:G>C	3B	787853986	0.0004483	0.103932584	178	1.298824398	3.834892882	3.348400834	YRH
YRH_Holeta	1342361 F 0-49:C>G-49:C>G	3D	399294085	0.0005372	0.151685393	178	1.298824398	4.123451177	3.26988268	YRH
YRH_Holeta	1228884 F 0-6:C>T-6:C>T	6B	664501564	8.96E-05	0.087078652	178	1.298824398	5.821044447	4.047782539	YRH
YRH_Holeta	1862737 F 0-44:C>G-44:C>G	6B	689032602	0.0008525	0.404494382	178	1.298824398	2.75385276	3.069308424	YRH
YRH_Holeta	1214898 F 0-48:C>A-48:C>A	7A	96563306	0.0005132	0.494382022	178	1.298824398	2.951941677	3.289702553	YRH
YRH_Holeta	2253374 F 0-35:G>A-35:G>A	7D	9295305	0.0007183	0.485955056	178	1.298824398	2.542356581	3.143671332	YRH
YRH_Holeta	981105 F 0-33:G>A-33:G>A	7D	13454220	0.000273	0.441011236	178	1.298824398	2.815146868	3.563831732	YRH
YRH_Holeta	1054974 F 0-30:A>C-30:A>C	7D	13606474	0.0006722	0.452247191	178	1.298824398	2.500012461	3.172523759	YRH
YRH_Meraro	1002704 F 0-50:T>C-50:T>C	2B	243083729	3.38E-07	0.193820225	178	8.852455549	6.898138908	6.470907967	YRH
YRH_Meraro	1072755 F 0-30:G>A-30:G>A	3A	733636208	0.0004563	0.306179775	178	9.361306333	4.883439759	3.34072475	YRH
YRH_Meraro	1051386 F 0-13:A>G-13:A>G	7D	353496936	0.0004469	0.151685393	178	9.784301521	7.389008932	3.349793744	YRH
YRH_Kulumsa	2294592 F 0-64:T>C-64:T>C	1B	73576935	0.0002959	0.04494382	178	11.16270958	9.90139023	3.528846802	YRH
YRH_Kulumsa	1209368 F 0-25:A>G-25:A>G	1B	687536131	0.0008341	0.137640449	178	10.65348915	6.535288921	3.078782458	YRH

YRH_Kulumsa	996534 F 0-32:A>G-32:A>G	1D	49605264	0.0004385	0.047752809	178	11.48010889	-	9.213248862	3.358043933	YRH
YRH_Kulumsa	4910323 F 0-27:C>A-27:C>A	1D	54339059	0.0001579	0.073033708	178	11.74320908	8.680586739	3.801573944	3.801573944	YRH
YRH_Kulumsa	1014633 F 0-11:A>G-11:A>G	4D	455618789	0.0006952	0.443820225	178	11.32602855	4.064027203	3.157908212	3.157908212	YRH
YRH_Kulumsa	2259257 F 0-11:A>C-11:A>C	6B	675702168	0.0006263	0.176966292	178	10.6734896	5.4682423	3.203213237	3.203213237	YRH
YRH_Kulumsa	1062073 F 0-41:C>T-41:C>T	7A	44352216	0.0009242	0.483146067	178	10.86119808	4.353822122	3.034235674	3.034235674	YRH
YRM_Combined	1094246 F 0-48:A>G-48:A>G	1A	337947849	0.0004086	0.120786517	178	10.96882357	7.620925201	3.388668349	3.388668349	YRM
YRM_Combined	2294592 F 0-64:T>C-64:T>C	1B	73576935	0.0008937	0.04494382	178	12.27824728	9.843464818	3.048794732	3.048794732	YRM
YRM_Holeta	986475 F 0-5:A>G-5:A>G	2B	74203726	0.0001186	0.379213483	178	7.150975084	5.312595632	3.925964686	3.925964686	YRM
YRM_Holeta	1007753 F 0-12:T>G-12:T>G	2B	237588008	0.0008249	0.146067416	178	7.239968603	-	5.615664803	3.083580378	YRM
YRM_Holeta	2264603 F 0-5:T>C-5:T>C	2B	759523837	0.0003448	0.469101124	178	10.34595223	5.111818822	3.462421582	3.462421582	YRM
YRM_Holeta	1245237 F 0-24:G>A-24:G>A	2B	759764778	0.0005044	0.449438202	178	7.097043424	4.845089017	3.29722171	3.29722171	YRM
YRM_Holeta	1115452 F 0-30:C>G-30:C>G	2B	760853647	0.0005123	0.483146067	178	9.126419705	4.838632081	3.290442427	3.290442427	YRM
YRM_Holeta	1073870 F 0-52:G>T-52:G>T	3A	250818410	0.0004491	0.188202247	178	7.144138569	6.106137813	3.347684813	3.347684813	YRM
YRM_Holeta	1207429 F 0-60:A>T-60:A>T	3A	639713075	0.0008847	0.129213483	178	7.184499277	7.36892938	3.053228316	3.053228316	YRM
YRM_Holeta	4989165 F 0-6:C>T-6:C>T	6A	51769657	0.0005669	0.132022472	178	9.760553411	6.662998478	3.246519691	3.246519691	YRM
YRM_Meraro	2249474 F 0-6:A>G-6:A>G	1B	561151613	0.0006473	0.078651685	178	8.529681479	-	7.558713774	3.188907878	YRM
YRM_Meraro	2249524 F 0-32:C>T-32:C>T	2D	576290797	2.24E-11	0.199438202	178	10.85789826	-10.0470021	10.65062601	10.65062601	YRM
YRM_Meraro	1072755 F 0-30:G>A-30:G>A	3A	733636208	1.52E-06	0.306179775	178	10.73955975	-	5.666550571	5.817595365	YRM
YRM_Meraro	1101425 F 0-12:G>A-12:G>A	3A	739951852	0.0001975	0.233146067	178	8.423553303	4.483289075	3.704385137	3.704385137	YRM
YRM_Meraro	3025953 F 0-25:G>A-25:G>A	4A	521603853	2.15E-13	0.16011236	178	9.964830726	11.9496768	12.66723386	12.66723386	YRM
YRM_Meraro	988680 F 0-37:C>T-37:C>T	4B	138472187	1.11E-09	0.157303371	178	11.78396595	10.09570388	8.954322171	8.954322171	YRM
YRM_Meraro	1228444 F 0-46:C>T-46:C>T	5A	36021495	0.0008416	0.244382022	178	9.632274249	4.388786733	3.074909171	3.074909171	YRM
YRM_Meraro	1113867 F 0-8:G>A-8:G>A	6B	687185128	0.0004299	0.146067416	178	8.819308499	-	6.489374497	3.366597542	YRM
YRM_Meraro	1216524 F 0-20:C>T-20:C>T	7A	730639307	3.59E-05	0.120786517	178	8.429832439	6.234440762	4.445346284	4.445346284	YRM

YRM_Kulumsa	1094246 F 0-48:A>G-48:A>G	1A	337947849	0.0006013	0.120786517	178	13.5744012	9.276284363	3.220937218	YRM
YRM_Kulumsa	2294592 F 0-64:T>C-64:T>C	1B	73576935	0.0003488	0.04494382	178	13.39923236	13.20486577	3.457479457	YRM
YRM_Kulumsa	1120791 F 0-30:A>G-30:A>G	1B	512632641	0.0007001	0.196629213	178	13.5744012	8.222023452	3.154831723	YRM
YRM_Kulumsa	996534 F 0-32:A>G-32:A>G	1D	49605264	0.0003896	0.047752809	178	13.5744012	12.53082782	3.409365552	YRM
YRM_Kulumsa	4910323 F 0-27:C>A-27:C>A	1D	54339059	0.000246	0.073033708	178	13.99983072	11.3803757	3.609033098	YRM
YRM_Kulumsa	1062073 F 0-41:C>T-41:C>T	7A	44352216	0.000949	0.483146067	178	13.5744012	5.859032952	3.022744906	YRM
YRMM_Combined	1094246 F 0-48:A>G-48:A>G	1A	337947849	0.00067	0.120786517	178	11.15300566	7.024367688	3.173949453	YRMM
YRMM_Holeta	986475 F 0-5:A>G-5:A>G	2B	74203726	0.0005563	0.379213483	178	10.72701423	4.535707855	3.254652312	YRMM
YRMM_Holeta	3064848 F 0-8:A>G-8:A>G	2B	454344609	0.0008534	0.221910112	178	10.01363215	4.803991678	3.068862327	YRMM
YRMM_Holeta	2279027 F 0-66:G>T-66:G>T	2B	647897009	0.0002873	0.179775281	178	11.03978263	5.921782369	3.54168006	YRMM
YRMM_Holeta	2264603 F 0-5:T>C-5:T>C	2B	759523837	0.0004331	0.469101124	178	10.91956505	4.765207132	3.363405174	YRMM
YRMM_Holeta	1115452 F 0-30:C>G-30:C>G	2B	760853647	0.0003368	0.483146067	178	10.23444005	4.724588865	3.472585453	YRMM
YRMM_Holeta	1207429 F 0-60:A>T-60:A>T	3A	639713075	0.0001779	0.129213483	178	10.78084533	7.832292613	3.749730453	YRMM
YRMM_Holeta	1108433 F 0-35:C>T-35:C>T	5A	429474426	0.0001384	0.148876404	178	12.74705938	6.766421689	3.858872165	YRMM
YRMM_Holeta	1214898 F 0-48:C>A-48:C>A	7A	96563306	0.0008336	0.494382022	178	10.11432717	4.668797026	3.079036074	YRMM
YRMM_Holeta	2246599 F 0-51:G>C-51:G>C	7D	14621383	0.0009737	0.47752809	178	11.46960567	4.057978583	3.011554683	YRMM
YRMM_Meraro	1115117 F 0-21:T>C-21:T>C	2B	743311212	0.0008798	0.407303371	178	8.710848987	6.730869079	3.055597417	YRMM
YRMM_Meraro	1072755 F 0-30:G>A-30:G>A	3A	733636208	0.0003088	0.306179775	178	9.809979922	7.057420477	3.510293347	YRMM
YRMM_Meraro	4003838 F 0-67:C>T-67:C>T	4B	15149905	0.000342	0.303370787	178	12.20623796	7.352085651	3.465953782	YRMM
YRMM_Meraro	3385417 F 0-31:C>G-31:C>G	4B	15752078	0.0005703	0.289325843	178	10.44440248	6.732925086	3.243879193	YRMM
YRMM_Meraro	3029334 F 0-20:G>A-20:G>A	6B	8235349	0.0002666	0.101123596	178	10.30588916	11.84161552	3.574200697	YRMM
YRMM_Kulumsa	1094246 F 0-48:A>G-48:A>G	1A	337947849	0.0004623	0.120786517	178	13.62764092	8.739937597	3.33510401	YRMM
YRMM_Kulumsa	2294592 F 0-64:T>C-64:T>C	1B	73576935	0.0003863	0.04494382	178	13.59018637	12.11605529	3.413101005	YRMM
YRMM_Kulumsa	996534 F 0-32:A>G-32:A>G	1D	49605264	0.0006116	0.047752809	178	13.14518254	-	3.213567234	YRMM

								11.20441293		
YRMM_Kulumsa	4910323 F 0-27:C>A-27:C>A	1D	54339059	0.0003267	0.073033708	178	13.62370674	10.31803112	3.485827832	YRMM
YRMM_Kulumsa	2259257 F 0-11:A>C-11:A>C	6B	675702168	0.0007573	0.176966292	178	10.72701423	6.715463889	3.120713703	YRMM
YRMM_Kulumsa	1062073 F 0-41:C>T-41:C>T	7A	44352216	0.0004152	0.483146067	178	13.1610438	5.764688116	3.381751363	YRMM
YRPH_Combined	1214020 F 0-68:A>C-68:A>C	1D	54911805	0.0004077	0.04494382	178	2.185954658	-	4.969182368	YRPH
YRPH_Combined	1016489 F 0-36:C>T-36:C>T	2A	750201766	0.0008153	0.084269663	178	11.98175305	3.433912192	3.088667909	YRPH
YRPH_Combined	2279027 F 0-66:G>T-66:G>T	2B	647897009	0.0007578	0.179775281	178	12.25987624	2.562107969	3.120418103	YRPH
YRPH_Combined	3064511 F 0-11:T>C-11:T>C	3A	516733247	0.0003347	0.18258427	178	11.33436879	2.713843599	3.475387519	YRPH
YRPH_Combined	980915 F 0-66:G>A-66:G>A	3A	517095336	0.0001474	0.297752809	178	11.0574837	2.178793728	3.831583392	YRPH
YRPH_Holeta	3020463 F 0-7:A>G-7:A>G	1D	7734813	0.0005989	0.238764045	178	2.185954658	-	1.893587749	YRPH
YRPH_Holeta	2279027 F 0-66:G>T-66:G>T	2B	647897009	0.0003495	0.179775281	178	2.185954658	2.376401356	3.456604345	YRPH
YRPH_Holeta	1201503 F 0-16:T>C-16:T>C	3A	565574116	0.0003974	0.168539326	178	2.185954658	2.282935855	3.400742289	YRPH
YRPH_Holeta	1342361 F 0-49:C>G-49:C>G	3D	399294085	0.0007645	0.151685393	178	2.185954658	2.678881826	3.116639471	YRPH
YRPH_Holeta	1118950 F 0-32:C>A-32:C>A	4A	603746204	0.0003318	0.348314607	178	2.185954658	-	2.098203484	YRPH
YRPH_Holeta	1862737 F 0-44:C>G-44:C>G	6B	689032602	0.0001684	0.404494382	178	10.966223	2.065690876	3.773577107	YRPH
YRPH_Kulumsa	2294592 F 0-64:T>C-64:T>C	1B	73576935	4.31E-07	0.04494382	178	13.39688484	6.774104784	6.365585879	YRPH
YRPH_Kulumsa	2278925 F 0-13:A>C-13:A>C	1B	605007601	0.0003402	0.199438202	178	11.27702815	2.975255736	3.46821364	YRPH
YRPH_Meraro	2282741 F 0-68:A>G-68:A>G	1A	481514973	0.0005986	0.393258427	178	10.7936183	-	3.489715283	YRPH
YRPH_Meraro	5969589 F 0-49:C>G-49:C>G	1D	244963962	0.0005772	0.157303371	178	14.13955234	-	4.234236727	YRPH
YRPH_Meraro	2261229 F 0-10:C>A-10:C>A	2B	727221588	0.0004262	0.314606742	178	10.27241072	4.095518918	3.370403596	YRPH
YRPH_Meraro	992248 F 0-39:T>C-39:T>C	5B	208728682	0.0006583	0.16011236	178	9.667482416	3.718999636	3.181570082	YRPH

Supplementary table 6. Putative QTLs identified across bread wheat chromosomes for yellow rust resistance, QTL= Quantitative trait locus; Chr = Chromosomes, MTAs = Marker trait associations, position* = position (Mbp) of the left flanking marker, Position** = position (Mbp) of right flanking marker, Phenotype_Location = yellow rust severity measured at individual or across location (Holetta, Kulumsa and Meraro), R2 = percentage of total phenotypic variance explained by the identified putative QTL. YRPH = coefficient of infection at pre-heading, YRH = coefficient of infection at heading, YRF = coefficient of infection at flowering, YRMM = coefficient of infection at mid-maturity, YRM = coefficient of infection at maturity

Putative QTL	Chr	Position (bp)	No.of MTAs	Flanking Markers			R-square	Phenotypes _Location
				Position*	Left /Right	Position** (Mbp)		
qYrS.01	1A	16417326	1	15807314	3957580 F 0-27:C>G-27:C>G/1144942 F 0-8:A>G-8:A>G	16914006	9.79	YRF_Combined
qYrS.02	1A	337947849	7	320331165	990732 F 0-35:C>A-35:C>A/1002101 F 0-39:C>T-39:C>T	339927631	10.57-13.63	YRM_Combined, YRM_Kulumsa, YRMM_Combined, YRMM_Kulumsa, YRPH_Meraro
qYrS.03	1A	512496605	2	512491703	2263444 F 0-36:A>G-36:A>G/1211261 F 0-25:T>C-25:T>C	513209052	10.53-10.74	YRF_Combined,
qYrS.04	1A	588261371	2	587860834	1274604 F 0-57:C>T-57:C>T/1224168 F 0-63:A>G-63:A>G	589629264	10.46-11.84	YRF_Combined, YRF_Meraro
qYrS.06	1B	73576935	6	72712433	3937513 F 0-44:A>C-44:A>C/1262351 F 0-27:C>A-27:C>A	83205362	10.53-13.59	YRM_Combined, YRM_Kulumsa, YRMM_Holeta, YRMM_Kulumsa & YRPH_Meraro
qYrS.07	1B	512632641-561151613	2	510601562	1713910 F 0-14:T>C-14:T>C/987187 F 0-28:C>G-28:C>G	561269842	8.53-13.57	YRM_Kulumsa & YRM_Meraro

qYrS.08	1B	605007601-687536131	2	604837044	1209708 F 0-39:C>T-39:C>T/2249179 F 0-42:T>G-42:T>G	2444404	10.65-1128	YRPH_Kulumsa & YRH_Kulumsa
qYrS.09	1D	7734813	2	6226459	1104052 F 0-5:A>G-5:A>G/3023474 F 0-6:C>T-6:C>T	9029459	1.30-2.19	YRH_Holeta & YRPH_Holeta
qYrS.10	1D	49605264-54911805	10	47652015	1127992 F 0-7:G>C-7:G>C/2242488 F 0-15:G>C-15:G>C	57506385	2.19-14.00	YRH_Kulumsa, YRM_Kulumsa, YRMM_Kulumsa, YRF_Kulumsa, YRH_Kulumsa & YRPH_Combined
qYrS.11	1D	244963962	1	238997014	2247033 F 0-5:A>T-5:A>T/1083752 F 0-19:G>A-19:G>A	261777240	14.14	YRPH_Meraro
qYrS.12	2A	733216778-750201766	2	731374489	7478588 F 0-11:C>G-11:C>G/1093498 F 0-43:G>T-43:G>T	750550903	10.74-1198	YRF_Holeta & YRPH_Combined
qYrS.13	2B	74203726	3	73990357	1025958 F 0-22:A>G-22:A>G/1204183 F 0-19:C>T-19:C>T	75832494	7.15-10.73	YRM_Holeta & YRMM_Holeta
qYrS.14	2B	237588008-243083729	3	237159653	1128307 F 0-57:G>T-57:G>T/3064852 F 0-14:G>A-14:G>A	249191759	7.24-10.53	YRM_Holeta, YRH_Combined & YRH_Meraro
qYrS.15	2B	410189157	1	409664071	1093481 F 0-22:C>T-22:C>T/4992185 F 0-35:C>T-35:C>T	410716788	11.69	YRF_Holeta
qYrS.16	2B	454344609	1	449468660	4910395 F 0-16:A>T-16:A>T/3534040 F 0-15:C>A-15:C>A	454848925	10.01	YRMM_Holeta
qYrS.17	2B	647897009	6	642790402	995800 F 0-30:A>G-30:A>G/982140 F 0-21:C>G-21:C>G	649534209	1.30-12.26	YRH_Combined, YRH_Holeta, YRMM_Holeta, YRPH_Combined & YRPH_Holeta
qYrS.18	2B	727221588	1	726135901	1028885 F 0-29:G>C-29:G>C/1009576 F 0-20:G>A-20:G>A	728953085	10.27	YRPH_Meraro
qYrS.19	2B	743311212	1	742460377	1232860 F 0-63:A>C-63:A>C/1096436 F 0-57:G>T-57:G>T	743320809	8.71	YRMM_Meraro

qYrS.20	2B	759523837-768053989	6	759175656	1190612 F 0-11:T>G-11:T>G/1090951 F 0-41:G>A-41:G>A	769262952	7.10-11.75	YRM_Holeta, YRMM_Holeta, YRM_Kulumsa, YRM_Holeta, YRMM_Holeta & YRF_Meraro
qYrS.21	2B	790748970-793146869	2	790748904	1218618 F 0-26:T>A-26:T>A/1211829 F 0-28:T>G-28:T>G	793517532	1.3	YRH_Holeta & YRH_Holeta
qYrS.22	2D	74936166	2	74929509	977602 F 0-51:A>G-51:A>G/2248376 F 0-64:A>G-64:A>G	75260741	9.374-10.24	YRF_Combined-
qYrS.23	2D	576290797	3	575705518	1249530 F 0-11:A>C-11:A>C/995850 F 0-55:G>C-55:G>C	576290863	10.856-13.11	YRM_Meraro &
qYrS.24	2D	591603469	1	591575616	5373802 F 0-11:T>C-11:T>C/1286277 F 0-52:A>G-52:A>G	593032041	11.65	YRF_Combined
qYrS.25	3A	250818410	4	235367940	5411362 F 0-51:G>A-51:G>A/1112462 F 0-18:G>A-18:G>A	257291100	7.14-10.58	YRF_Holeta, , & YRM_Holeta
qYrS.26	3A	565574116	1	565456003	1133347 F 0-53:T>C-53:T>C/1237190 F 0-7:T>C-7:T>C	572529998	1.19	YRPH_Holeta
qYrS.27	3A	639713075	4	639656543	2279154 F 0-27:C>T-27:C>T/1040728 F 0-65:T>C-65:T>C	640448153	7.184-10.78	YRF_Holeta, , & YRMM_Holeta
qYrS.28	3A	733636208-739951852	5	733330304	991604 F 0-46:A>G-46:A>G/2265277 F 0-35:A>C-35:A>C	739975284	8.42-10.74	YRH_Meraro, YRM_Meraro, YRMM_Meraro & YRM_Meraro
qYrS.29	3B	20999249	1	20826251	1135829 F 0-43:C>G-43:C>G/1089285 F 0-12:G>A-12:G>A	21863643	10.43	YRF_Combined
qYrS.32	3B	463461507	2	463202357	5325155 F 0-26:G>T-26:G>T/1020069 F 0-64:G>A-64:G>A	473708936	12.15-14.05	YRF_Meraro &
qYrS.33	3B	787853986	1	787810930	1039960 F 0-7:C>T-7:C>T/1090137 F 0-37:C>A-37:C>A	788195824	1.3	YRH_Holeta
qYrS.34	3D	339476105	3	337247920	994556 F 0-12:C>T-12:C>T/3937988 F 0-67:G>A-67:G>A	349111387	1.30-11.65	YRH_Kulumsa & YRPH_Holeta

qYrS.35	3D	569281482	1	568871407	2259787 F 0-7:A>G-7:A>G/1218288 F 0-20:A>G-20:A>G	571054885	10.21	YRF_Combined
qYrS.36	4A	521603853	1	520685128	100763811 F 0-27:T>C-27:T>C/1165073 F 0-36:T>C-36:T>C	531682048	9.96	YRM_Meraro
qYrS.37	4A	603746204	1	601841436	1397352 F 0-18:C>G-18:C>G/2255861 F 0-31:A>G-31:A>G	608072436	2.19	YRPH_Holeta
qYrS.38	4B	15149905	2	14841843	1240150 F 0-12:G>A-12:G>A/3034460 F 0-13:T>C-13:T>C	15183909	10.44-12.21	YRMM_Meraro & YRMM_Meraro
qYrS.39	4B	66799362	2	64807791	1016230 F 0-27:T>G-27:T>G/1110379 F 0-38:C>A-38:C>A	67006437	11.75-11.79	YRF_Meraro &
qYrS.40	4B	138472187	1	134824702	1026550 F 0-42:T>C-42:T>C/5323926 F 0-23:C>T-23:C>T	139546263	11.78	YRM_Meraro
qYrS.41	4D	455618789	1	455472305	3027622 F 0-8:G>A-8:G>A/1173173 F 0-5:C>T-5:C>T	456054444	11.33	YRH_Kulumsa
qYrS.42	5A	36021495	5	34657513	995502 F 0-8:C>T-8:C>T/1128589 F 0-27:T>C-27:T>C	36365068	9.16-12.13	YRM_Meraro, YRF_Combined, YRF_Meraro, & YRF_Combined
qYrS.43	5A	429474426	3	417313880	4260954 F 0-26:C>T-26:C>T/1703104 F 0-27:T>C-27:T>C	436890364	10.04-12.75	YRF_Holeta, & YRMM_Holeta
qYrS.44	5B	208728682	1	194139661	7336013 F 0-20:G>A-20:G>A/993622 F 0-21:C>T-21:C>T	228277789	3.718999636	YRPH_Meraro
qYrS.45	5D	515407161	1	515042025	1072421 F 0-31:T>C-31:T>C/4003049 F 0-20:G>A-20:G>A	515411132	13.12	YRF_Meraro
qYrS.46	5D	529525683	1	529227968	1074650 F 0-5:A>G-5:A>G/1021513 F 0-60:G>A-60:G>A	529525749	11.55	YRF_Meraro
qYrS.47	5D	533205336	1	533198477	1091544 F 0-62:C>T-62:C>T/1045790 F 0-38:G>A-38:G>A	533544970	9.76	YRM_Holeta
qYrS.48	6A	51769657	1	49768768	1002532 F 0-61:T>A-61:T>A/19484471 F 0-29:C>T-29:C>T	51769657	10.31	YRMM_Meraro
qYrS.49	6B	8235349	1	8049236	995807 F 0-17:C>T-17:C>T/3029334 F 0-20:G>A-20:G>A	8235349	12.53	YRF_Meraro

qYrS.50	6B	291067106	1	290201782	1018874 F 0-36:G>A-36:G>A/1035461 F 0-39:T>C-39:T>C	301571656	11.68	YRF_Meraro
qYrS.51	6B	476032032-583215607	2	474821849	998394 F 0-24:G>A-24:G>A/1106830 F 0-19:C>T-19:C>T	583334012	11.68-11.83	YRF_Meraro
qYrS.52	6B	664501564	1	664457926	1021674 F 0-67:C>T-67:C>T/1012196 F 0-18:A>C-18:A>C	665128011	1.3	YRH_Holeta
qYrS.53	6B	675702168	6	675620421	3022065 F 0-20:G>A-20:G>A/2255000 F 0-37:T>C-37:T>C	676163297	1.30-10.97	YRH_Kulumsa, YRMM_Kulumsa, YRM_Meraro, YRF_Holeta & YRPH_Holeta
qYrS.54	7A	12800907-50346076	7	12099978	984908 F 0-65:C>T-65:C>TT/1201828 F 0-47:T>C-47:T>C	50346346	9.1556-13.57	YRF_Kulumsa, YRH_Kulumsa, YRM_Kulumsa, YRMM_Kulumsa & YRF_Meraro
qYrS.55	7A	96563306-128909455	5	95895534	1036504 F 0-9:C>T-9:C>T/982709 F 0-31:G>A-31:G>A	128969214	1.30-12.14	YRF_Holeta, YRH_Holeta, YRMM_Holeta & YRF_Meraro
qYrS.56	7D	9295305-14621383	7	7744813	4911180 F 0-7:A>T-7:A>T/1076917 F 0-55:G>A-55:G>A	14767599	1.30-11.47	YRH_Holeta, YRH_Holeta, YRH_Holeta, YRF_Holeta, & YRMM_Holeta
qYrS.58	7D	353496936		351629441	100564434 F 0-8:T>C-8:T>C/1104290 F 0-22:T>C-22:T>C	353497260	9.78	YRH_Meraro

Supplementary table 7. High confidence genes and gene models detected within the identified yellow rust resistance associated QTL regions, High confident genes annotated from IWGSC CS RefSeq ver. 1.0 IWGSC Annotation v.2.1 available at https://wheat_x005furgi.versailles.inrae.fr/Seq-Repository/Annotations. Retrieved on May 12,2023.

Putative QTL	Chr	Position (bp)	Range	Gene ID	Gene position			Gene Ontology (Biological process)
					Start	End	strand	
qYrS.01	1A	16417326	15917326-21417326	TraesCS1A02G033600	16407008	16407008	+	defense response to bacterium
				TraesCS1A02G035400	18493615	18494853	-	response to stress
				TraesCS1A02G035600	19062157	19063423	-	defense response.
				TraesCS1A02G036300	20179711	20183942	+	egative regulation of leaf senescence.
				TraesCS1A02G037300	20888601	20889881	-	associated to induced systemic resistance
qYrS.02	1A	337947849	332947849-342947849	TraesCS1A02G189700	43395336	343397180	-	immune response
				TraesCS1A02G183400	333134461	333139522	-	systemic acquired resistance, salicylic acid mediated signaling pathway
				TraesCS1A02G189900	343615952	343618536	+	associated to cellular response to oxidative stress
				TraesCS1A02G183900	333868548	333886602	+	immune response-regulating cell surface receptor signaling pathway
				TraesCS1A02G184700	335115860	335116228	+	response to stress
qYrS.03	1A	512496605	511996605-	TraesCS1A02G189100	342387315	342391668	+	ubiquitin-protein transferase activity, ubiquitin-dependent protein catabolic process, protein autoubiquitination
				TraesCS1A02G322200	512871688	512874242	+	response to biotic stimulus, associated to

			517496605					defense response
				TraesCS1A02G325100	516040780	516041316	-	induction by symbiont of host immune response.
				TraesCS1A02G325400	516369536	516373444	+	defense response to fungus
				TraesCS1A02G325600	516430393	516432298	+	response to microbial phytotoxin
				TraesCS1A02G325900	516563565	516574801	-	innate immune response
				TraesCS1A02G327700	517095424	517101137	-	cellular response to stress
				TraesCS1A02G327900	517186972	517187646	-	immune effector process, activation of immune response
qYrS.04	1A	588261371	587761371-593261371	TraesCS1A02G441200	589820460	589822655	+	response to symbiotic fungus
				TraesCS1A02G445600	593295227	593301920	+	response to stimulus
				TraesCS1A02G444300	592313029	592316609	-	response to oxidative stress.
qYrS.06	1B	73576935	73076935-78576935	TraesCS1B02G086600	74226370	74234563	+	regulation of leaf senescence
				TraesCS1B02G086400	72246455	72247251	+	response to stimulus
qYrS.07	1B	512632641-561151613	507632641-566151613	TraesCS1B02G333500	560018875	560021191	-	to response to stress
				TraesCS1B02G333600	560175742	560178662	-	response to molecule of fungal origin
				TraesCS1B02G334900	561752758	561754260	-	to response to stress
				TraesCS1B02G30540	528358456	528360309	-	ubiquitin-protein transferase activity, ubiquitin-dependent protein catabolic process, protein autoubiquitination
				TraesCS1B02G308400	531004951	531012830	-	response to endogenous stimulus, protein ubiquitination, SCF-dependent proteasomal ubiquitin-dependent protein catabolic process, obsolete multi-organism process, SCF ubiquitin ligase complex
				TraesCS1B02G312700	536601760	536605386	+	modulation by virus of host process, multi-organism reproductive process,

								transport of virus in multicellular host
				TraesCS1B02G324300	549790711	549794806	+	MAPK cascade, respiratory burst involved in defense response, regulation of response to biotic stimulus, detection of biotic stimulus, systemic acquired resistance, salicylic acid mediated signaling pathway, regulation of plant-type hypersensitive response, negative regulation of defense response, defense response to bacterium, defense response to bacterium, obsolete regulation of multi-organism process, obsolete multi-organism process,
				TraesCS1B02G326600	552473380	552474529	-	respiratory burst involved in defense response, induced systemic resistance, jasmonic acid mediated signaling pathway
qYrS.08	1B	605007601 - 687536131	600007601- 692536131	TraesCS1B02G371600	601267754	601268098	+	immune response-activating signaling pathway
				TraesCS1B02G375100	5933187	605936260	-	response to symbiotic fungus
				TraesCS1B02G479100	687088286	687093181	-	to defense response.
				TraesCS1B02G480300	687785481	687789175	+	regulation of defense response, systemic acquired resistance
				TraesCS1B02G403500	633120478	633133515	-	defense response, response to biotic stimulus
				TraesCS1B02G442700	663607263	663612119	-	ubiquitin-protein transferase activity, ubiquitin-dependent protein catabolic process, protein autoubiquitination, response to stressSCF-dependent proteasomal ubiquitin-dependent protein catabolic process, obsolete multi-organism process, ubiquitin ligase

								complex,
				TraesCS1B02G475800	684096801	684098680	-	response to stress, obsolete multi-organism process
				TraesCS1B02G445800	665853937	665854986	-	defense response
				TraesCS1B02G440300	661929604	661930887	+	response to biotic stimulus, response to stress, obsolete multi-organism process
qYrS.09	1D	7734813	7234813-12734813	TraesCS1D02G018500	8014222	8016565	+	systemic acquired resistance, defense response to fungus
				TraesCS1D02G019800	8618358	8619547	-	defense response, response to abiotic stimulus
				TraesCS1D02G031100	12248604	12250931	-	defense response, response to fungus
				TraesCS1D02G019500	8473982	8474961	+	defense response
				TraesCS1D02G030300	11780392	11783116	-	respiratory burst involved in defense response, proteasome-mediated ubiquitin-dependent protein catabolic process., protein autoubiquitination, ubiquitin protein ligase activity
				TraesCS1D02G024600	10367753	10372465	+	defense response to bacterium
				TraesCS1D02G018700	8182627	8186066	-	defense response, response to biotic stimulus, obsolete multi-organism process
qYrS.10	1D	49605264-54911805	44605264-59911805	TraesCS1D02G060900	41300268	41302531	-	cellular response to stress
				TraesCS1D02G063100	43233811	43234041	-	response to stress
				TraesCS1D02G066000	47706578	47716370	+	regulation of cellular response to stress
				TraesCS1D02G066700	48380218	48401734	+	to defense response
				TraesCS1D02G070500	51830243	51830506	-	cellular response to stress.
qYrS.11	1D	244963962	244463962-249963962	TraesCS1D02G172000	245975372	245976949	-	defense response
				TraesCS1D02G173900	247507055	247507648	-	defense response to fungus
qYrS.12	2A	733216778-	728216778-755201766	TraesCS2A02G500800	729540713	729546699	-	defense response

		750201766						
				TraesCS2A02G502600	731373672	731375084	+	response to stress
				TraesCS2A02G505900	734087112	734090432	+	cellular response to stress
				TraesCS2A02G506500	734347340	734352307	-	defense response
				TraesCS2A02G512100	737046055	737049316	+	defense response to fungus
				TraesCS2A02G526400	746753763	746755926	+	defense response
				TraesCS2A02G522200	744638919	744642776	-	ubiquitin-protein transferase activity, response to stimulus, protein autoubiquitination
				TraesCS2A02G540000	752103126	752106987	-	systemic acquired resistance, salicylic acid mediated signaling pathway, obsolete multi-organism process
				TraesCS2A02G533700	749523738	749525258	+	response to fungus, obsolete multi-organism process
qYrS.13	2B	74203726	73703726-79203726	TraesCS2B02G111900	74204074	74205175	+	negative regulation of defense response
				TraesCS2B02G112200	75609123	75614956	-	response to stress
				TraesCS2B02G112400	75691886	75695689	+	host response to induction by symbiont of tumor, nodule or growth in host
				TraesCS2B02G113200	76816411	76823435	-	systemic acquired resistance
qYrS.14	2B	237588008 - 243083729	232588008-248083729	TraesCS2B02G234900	234364362	234369521	-	response to stress
				TraesCS2B02G235700	236045070	236048639	+	response to stress
				TraesCS2B02G23670	237343301	237348967	+	response to molecule of fungal origin
				TraesCS2B02G238000	239194939	239197833	-	immune effector process, cellular response to stress
qYrS.15	2B	410189157	409689157-415189157	TraesCS2B02G295900	412776786	412781546	-	response to stress
				TraesCS2B02G296300	413446010	413447950	+	defense response
				TraesCS2B02G294500	411140309	411143734	-	response to stimulus
				TraesCS2B02G296000	412989047	412992654	+	response to nematode, obsolete multi-

								organism process,
				TraesCS2B02G295300	412399514	412402350	+	response to stimulus
qYrS.16	2B	454344609	453844609- 459344609	TraesCS2B02G318600	454342642	454344854	-	response to stress
				TraesCS2B02G318000	453809195	453813696	+	ubiquitin-dependent protein catabolic process, protein deubiquitination
				TraesCS2B02G319400	454927424	454927537	-	response to stimulus, obsolete oxidation- reduction process
				TraesCS2B02G321500	458621788	458626611	-	response to stress
qYrS.17	2B	647897009	647397009- 652897009	raesCS2B02G454700	649656198	649656461	-	response to stress
				TraesCS2B02G453600	647451070	647451267	+	response to stress
				TraesCS2B02G454000	648073433	648085027	+	respiratory burst involved in defense response, response to nematode
				TraesCS2B02G454600	649479177	649480859	-	response to stimulus
qYrS.18	2B	727221588	726721588- 732221588	TraesCS2B02G455500	650164651	650165049	+	response to stress
				TraesCS2B02G455900	650399573	650405456	+	response to stress
				TraesCS2B02G456700	651554252	651557192	+	response to other organism
				TraesCS2B02G532700	728559987	728562235	-	response to stimulus
				TraesCS2B02G533800	730079440	730083075	-	systemic acquired resistance
				TraesCS2B02G534600	730848622	730852822	-	response to nematode, regulation of plant-type hypersensitive response
				TraesCS2B02G535000	731250064	731252586	+	response to virus, response to bacterium, systemic acquired resistance,
				TraesCS2B02G535600	731480831	731482520	-	defense response to bacterium, obsolete multi-organism proces
qYrS.19	2B	743311212	742811212- 748311212	TraesCS2B02G546700	743726671	743727513	+	defense respons
				TraesCS2B02G550300	746108243	746115902	-	response to stress
				TraesCS2B02G552000	747920882	747921157	-	response to stress
				TraesCS2B02G548300	744372539	744375320	-	protein deubiquitination, ubiquitin-

								dependent protein catabolic process
				TraesCS2B02G548900	744856112	744857194	-	defense response to fungus, response to bacterium, obsolete multi-organism process
				TraesCS2B02G549800	745771187	745773385	-	leaf senescence
				TraesCS2B02G551200	747180304	747181959	-	response to stress
qYrS.20	2B	759523837 - 768053989	754523837- 773053989	TraesCS2B02G564300	756156764	756157078	-	immune respons
				TraesCS2B02G564800	756552584	756553403	-	response to stress
				TraesCS2B02G565800	757209680	757215124	+	defense response
				TraesCS2B02G565900	757219691	757221624	-	defense response
				TraesCS2B02G566800	758084174	758085608	-	response to fungus
				TraesCS2B02G572500	762213310	762214734	-	defense response
				TraesCS2B02G576000	765063856	765068560	+	response to stress
				TraesCS2B02G576700	765454852	765461696	+	induced systemic resistance
				TraesCS2B02G579800	767651333	767657210	-	cellular response to stress
				TraesCS2B02G580800	768289431	768293206	+	innate immune response
				TraesCS2B02G583600	770765277	770767674	-	systemic acquired resistance, salicylic acid mediated signaling pathwa
qYrS.21	2B	790748970 - 793146869	785748970- 798146869	TraesCS2B02G606000	787098355	787098786	+	defense response to fungus
				TraesCS2B02G60880	789119521	789134807	-	defense response, response to biotic stimulus
				TraesCS2B02G608500	788797163	788804836	+	defense response, response to other organism
				TraesCS2B02G608700	788873144	788874300	+	response to stress
				TraesCS2B02G608800	789119521	789134807	-	defense response, response to biotic stimulus
				TraesCS2B02G608900	789263450	789265949	-	response to stress
				TraesCS2B02G609500	789605346	789606492	-	response to oxidative stress

				TraesCS2B02G610100	789790100	789792327	+	response to stress
				TraesCS2B02G610800	790439835	790443262	+	response to stress
				TraesCS2B02G611200	790612843	790613405	+	response to stress
				TraesCS2B02G611300	790623664	790624261	+	response to stress
				TraesCS2B02G620500	794963403	794988705	+	defense response
qYrS.22	2D	74936166	74436166- 79936166	TraesCS2D02G127900	74524949	74526393	-	response to stress
				TraesCS2D02G128100	74848324	74862386	+	response to stress
				TraesCS2D02G128200	74927033	74929790	+	response to stress
				TraesCS2D02G132600	77378971	77383706	-	response to stress
				raesCS2D02G132900	78375985	78392563	+	defense response to bacterium
				TraesCS2D02G133800	78755770	78758700	+	response to stimulus
qYrS.23	2D	576290797	575790797- 581290797	TraesCS2D02G472600	576204362	576206685	-	obsolete pathogenesis
				TraesCS2D02G472500	576192669	576196949	-	response to stress
				TraesCS2D02G473300	577076410	577078486	-	response to oxidative stress
				TraesCS2D02G474200	577440621	577443620	+	response to stimulus
				TraesCS2D02G475600	578002784	578005175	+	response to stress
				TraesCS2D02G476300	578703645	578704289	+	defense response, response to other organism,
				TraesCS2D02G476400	578888496	578889264	+	defense response, response to biotic stimulus
				TraesCS2D02G477800	579517093	579521619	-	response to stimulus
				TraesCS2D02G480000	580783803	580785165	+	cellular response to stress
qYrS.24	2D	591603469	591103469- 596603469	TraesCS2D02G493800	591178104	591179288	+	response to stress
				TraesCS2D02G494900	591955834	591973038	-	response to stimulus
				TraesCS2D02G495900	592618725	592622863	-	defense response, response to biotic stimulus
				TraesCS2D02G496300	592635145	592639656	-	immune response-regulating signaling pathway, detection of external stimulus, plant-type hypersensitive response,

								detection of bacterium, defense response to bacterium
				TraesCS2D02G496500	592790485	592791849	-	response to stress
				TraesCS2D02G497400	593270400	593275755	-	defense response to fungus, regulation of plant-type hypersensitive response, negative regulation of defense response
				TraesCS2D02G497600	593370558	593373483	+	response to stress
				TraesCS2D02G498100	593683638	593696248	+	response to stress
				TraesCS2D02G498400	593851400	593852689	+	response to stimulus
				TraesCS2D02G499400	594482398	594484623	-	positive regulation of immune system process, response to stress
				TraesCS2D02G500400	595145351	595149710	+	defense response to bacterium
				TraesCS2D02G501500	595556938	595557531	+	response to stimulus
				TraesCS2D02G501800	596029404	596031088	+	defense response
				TraesCS2D02G502700	596252069	596254635	-	response to molecule of fungal origin
qYrS.25	3A	250818410	250318410-265818410	TraesCS3A02G192600	256234246	256245579	-	plant-type hypersensitive response, positive regulation of defense response to oomycetes
qYrS.26	3A	565574116	565074116-570574116	TraesCS3A02G321700	565351615	565357417	+	response to stimulus
				TraesCS3A02G322100	565765947	565773872	+	response to stimulus
				TraesCS3A02G323900	568424166	568425588	+	response to stress, cellular response to stimulus
				TraesCS3A02G323800	568380859	568383686	+	response to stress
				TraesCS3A02G324100	568663686	568666242	+	negative regulation of defense response
				TraesCS3A02G325200	569890845	569892111	+	regulation of plant-type hypersensitive response, GO:0010363
qYrS.27	3A	639713075	639213075-644713075	TraesCS3A02G391800	639490139	639505143	+	defense response to virus
				TraesCS3A02G392800	640679084	640702807	-	response to stimulus
				TraesCS3A02G393200	641012141	641013235	+	associated to response to stress
				TraesCS3A02G394400	642031992	642034460	-	defense response to bacterium

				TraesCS3A02G394700	642158665	642160126	+	response to stress
				TraesCS3A02G395300	642680542	642682224	-	defense response to fungus, innate immune response, negative regulation of defense response, obsolete multi-organism process, leaf senescence
				TraesCS3A02G396000	643209171	643210809	-	response to stress, cellular response to endogenous stimulus
				TraesCS3A02G396200	643459970	643461316	-	response to stress
qYrS.28	3A	733636208 - 739951852	728636208- 744951852	TraesCS3A02G509800	730177399	730178426	-	response to stress
				TraesCS3A02G511400	730937527	730940572	-	cellular response to biotic stimulus, filamentous growth of a population of unicellular organisms in response to biotic stimulus
				TraesCS3A02G511700	731083694	731089749	+	defense response to fungus, defense response to fungus, response to endoplasmic reticulum stress, response to endoplasmic reticulum stress, detection of biotic stimulus, plant-type hypersensitive response, respiratory burst involved in defense response
				TraesCS3A02G513100	732475913	732485301	-	defense response to fungus
				TraesCS3A02G516500	734003472	734004327	-	response to stress
				TraesCS3A02G518900	736081968	736082514	-	response to stress
				TraesCS3A02G519100	737114170	737114739	+	defense response
				TraesCS3A02G519900	737289221	737290303	+	defense response, response to other organism
				TraesCS3A02G520100	737315606	737317297	+	response to stress
				TraesCS3A02G521400	737994803	737995873	+	response to stimulus
				TraesCS3A02G521500	738129361	738132878	+	response to stress, response to virus, obsolete multi-organism process

				TraesCS3A02G519100	737114170..	737114739	+	defense response
				TraesCS3A02G51990	737289221	737290303	+	defense response, response to other organism
				TraesCS3A02G521200	737892326	737897743	+	response to stress
				TraesCS3A02G521500	738129361	738132878	+	response to stress, response to virus,obsolete multi-organism process
				TraesCS3A02G524000	739158541	73916085	-	defense response to bacterium, obsolete multi-organism process
				TraesCS3A02G524400	739276714	739278923	+	immune system process
				TraesCS3A02G524500	739309245	739309931	+	response to stress
				TraesCS3A02G526900	740747649	740748836	+	response to stress, response to endogenous stimulus, response to organic substance, obsolete multi-organism process
qYrS.29	3B	20999249	20499249-25999249	TraesCS3B02G041900	20840849	2084289	-	defense response to fungus, obsolete multi-organism process, defense response to bacterium, response to endoplasmic reticulum stress, negative regulation of defense response, detection of bacterium, systemic acquired resistance, salicylic acid mediated signaling pathway, regulation of response to biotic stimulus
				TraesCS3B02G042300	21402835	21405805	+	response to bacterium, obsolete multi-organism process
				TraesCS3B02G042500	21880115	21880378	+	immune response, immune response-regulating cell surface receptor signaling pathway, response to stress
				TraesCS3B02G044600	22665916	22667524	-	response to stress
				TraesCS3B02G045900	23182497	23193752	+	defense response to fungus, obsolete multi-organism process, obsolete regulation of multi-organism process, defense response to bacterium, negative regulation of defense response,

								regulation of plant-type hypersensitive response, detection of biotic stimulus, detection of external stimulus,
				TraesCS3B02G046400	23692602	23693870	-	response to stress, obsolete multi-organism process
				TraesCS3B02G046800	23781928	23787160	-	response to stress, obsolete multi-organism process
				TraesCS3B02G047000	23943718	23945640	-	response to stress
				TraesCS3B02G050400	25247737	25249486	-	defense response
qYrS.32	3B	463461507	462961507-468461507	TraesCS3B02G289400	464504372	464505445	-	response to stress
				TraesCS3B02G290800	466296792	466299934	+	response to stress, response to other organism
qYrS.33	3B	787853986	787353986-792853986	TraesCS3B02G553300	787889744	787891127	+	response to stimulus
				TraesCS3B02G553500	787990137	787990863	-	response to fungus
				TraesCS3B02G553800	788058123	788058587	-	response to fungus
				TraesCS3B02G553900	788072828	788073684	-	response to fungus, obsolete multi-organism process
				TraesCS3B02G554100	788138799	788153828	+	response to fungus
				TraesCS3B02G554500	788252246	788259997	-	defense response, response to biotic stimulus, obsolete multi-organism process
				TraesCS3B02G555900	789322601	789324296	-	response to stimulus, obsolete multi-organism process
				TraesCS3B02G556100	789497688	789501812	-	response to stress
				TraesCS3B02G556300	790370098	790371132	-	response to stress
				TraesCS3B02G556900	790744026	790751732	-	defense response, response to biotic stimulus
				TraesCS3B02G557100	791250534	791254302	+	defense response, response to other organism
				TraesCS3B02G557201	791280668	791287389	+	defense response, response to other

								organism
				TraesCS3B02G557300	791636071	791642000	+	defense response to fungus, defense response, response to other organism, regulation of response to biotic stimulus, detection of external stimulus, plant-type hypersensitive response, negative regulation of defense response, obsolete regulation of multi-organism process, obsolete multi-organism process
				TraesCS3B02G557500	791659156	791665971	+	defense response, obsolete multi-organism process, response to other organism
				TraesCS3B02G557900	792343892	792344128	-	immune response, response to external stimulus
qYrS.34	3D	339476105	338976105-344476105	TraesCS3D02G243700	338945505	338946500	+	response to stress
				TraesCS3D02G246000	342516916	342521973	-	response to fungus, leaf senescence, regulation of plant-type hypersensitive response, defense response to bacterium
qYrS.35	3D	569281482	568781482-574281482	TraesCS3D02G461200	565819706	565821322	-	defense response to fungus, leaf senescence
				TraesCS3D02G461300	565830663	565832428	+	response to stress
				TraesCS3D02G461600	566100597	566103750	-	immune response, response to external stimulus
				TraesCS3D02G462400	566954788	566955711	+	response to stress
				TraesCS3D02G462500	567063391	567065164	-	response to stimulus
				TraesCS3D02G463100	567218912	567220299	-	response to stress
				TraesCS3D02G463200	567222972	567224129	-	response to stress
				TraesCS3D02G463400	567300833	567301981	-	response to stress
				TraesCS3D02G463500	567662527	567664450	-	response to stress
				TraesCS3D02G463900	567902730	567903851	+	response to stress
				TraesCS3D02G465000	568836712	568837491	-	innate immune response

				TraesCS3D02G465100	568841994	568849330	-	innate immune response
				TraesCS3D02G465200	569118263	569119647	-	immune response, response to stress, obsolete multi-organism process
				TraesCS3D02G465400	569132339	569134633	+	immune effector process, cellular response to stress
qYrS.36	4A	521603853	521103853-526603853	TraesCS4A02G219100	521557960	52156334	-	response to stress
				TraesCS4A02G219100	521557960	521563349	-	response to stress
				TraesCS4A02G219700	521917748	521920022	-	response to fungus
				TraesCS4A02G220300	523446892	523455917	-	response to stress
				TraesCS4A02G220600	524272281	524273502	-	immune system process.
				TraesCS4A02G221100	525736492	525738125	-	response to stimulus
qYrS.37	4A	603746204	603246204-608746204	TraesCS4A02G310600	603372580	603375220	-	response to stress
				TraesCS4A02G311500	603469204	603469938	+	response to stimulus
				TraesCS4A02G311800	603496846	603499370	-	response to stress
				TraesCS4A02G312500	603634586	603635579	-	regulation of defense response to fungus
				TraesCS4A02G312900	603698121	603703864	+	defense response, response to other organism
				TraesCS4A02G314300	604772917	604775106	+	defense response, response to other organism
				TraesCS4A02G314400	604845889	604850471	-	defense response, defense response, obsolete multi-organism process
				TraesCS4A02G314600	604940912	604941475	+	defense response
				TraesCS4A02G315700	605711154	605714476	+	response to stress
				TraesCS4A02G317000	606591102	606591425	+	response to stress
				TraesCS4A02G318000	607178696	607179542	+	cellular response to extracellular stimulus
				TraesCS4A02G318400	607309139	607310644	-	defense response
				TraesCS4A02G319300	608265657	608272622	-	defense response, response to biotic stimulus, obsolete multi-organism process

				TraesCS4A02G319400	608479107	608481104	-	defense response, response to other organism, obsolete multi-organism process
qYrS.38	4B	15149905	14649905-20149905	TraesCS4B02G023000	16871065	16871863	-	response to stress, cellular response to stimulus
				TraesCS4B02G023200	16894955	16895287	-	response to stress
				TraesCS4B02G023700	17083214	17084527	+	response to fungus
				TraesCS4B02G023800	17090710	17097482	+	detection of external stimulus, detection of bacterium, obsolete multi-organism process
				TraesCS4B02G02500	17822364	17825846	+	response to stimulus
qYrS.39	4B	66799362	66299362-71799362	TraesCS4B02G071900	66471308	66473015	-	response to stress, programmed cell death, positive regulation of programmed cell death
				TraesCS4B02G073000	68124629	68125012	-	response to stress
				TraesCS4B02G073100	68358124	68362621	+	response to stimulus
				TraesCS4B02G07350	68720794	68721168	+	response to stress, cell death. regulation of programmed cell death
				raesCS4B02G074400	69889803	69891450	-	defense response to fungus, innate immune response, obsolete multi-organism process, negative regulation of defense response, regulation of plant-type hypersensitive response,
				TraesCS4B02G074500	70055606	70056994	-	defense response to fungus, innate immune response, leaf senescence, regulation of plant-type hypersensitive response, negative regulation of cell growth, negative regulation of defense response, negative regulation of defense response,
				TraesCS4B02G075200	71244991	71247199	-	response to stress
				TraesCS4B02G075800	71753866	71754522	+	cellular response to stress

qYrS.40	4B	138472187	137972187- 143472187	TraesCS4B02G118400	138615697	138618444	-	cellular response to stress
				TraesCS4B02G118800	139137793	139138864	-	response to stress
				TraesCS4B02G120900	142541428	142541793	+	defense response
				TraesCS4B02G120800	142518084	142523663	+	defense response to fungus, detection of biotic stimulus, plant-type hypersensitive response, negative regulation of defense response, response to endoplasmic reticulum stress, defense response to bacterium, negative regulation of programmed cell death, negative regulation of programmed cell death, cellular response to biotic stimulus
				TraesCS4B02G120900	142541428	142541793	+	defense response
				TraesCS4B02G121000	142674471	142675019	+	defense response
				TraesCS4B02G121500	143312969	143315845	-	response to stress, response to biotic stimulus
qYrS.41	4D	455618789	455118789- 460618789	TraesCS4D02G284000	455599799	455602536	+	response to stimulus
				TraesCS4D02G286100	456493885	456497502	-	defense response to fungus, obsolete multi-organism process
				TraesCS4D02G286300	456690657	456691795	-	response to stress
				TraesCS4D02G286500	457500939	457506583	-	response to fungus
				TraesCS4D02G286700	458384021	458385084	+	to response to symbiotic fungus
				TraesCS4D02G287000	459054432	459059542	+	defense response
				TraesCS4D02G287300	459068393	459068879	+	immune system process, response to stimulus
				TraesCS4D02G287400	459074666	459080954	-	filamentous growth of a population of unicellular organisms in response to biotic stimulus, cellular response to biotic stimulus
				TraesCS4D02G287800	459301169	459301528	-	response to stress, response to bacterium

				TraesCS4D02G288900	459685649	459686959	+	response to stress, cellular response to stimulus
qYrS.42	5A	36021495	35521495-41021495	TraesCS5A02G038400	35639269	35640938	-	response to stress
				TraesCS5A02G040100	36329350	36332127	+	defense response
				TraesCS5A02G041200	37082178	37082796	+	response to stress
				TraesCS5A02G043000	38796605	38797971	+	response to stimulus
				TraesCS5A02G043800	40163148	40167710	-	response to fungus, response to nematode, defense response to Gram-negative bacterium, obsolete multi-organism process
				TraesCS5A02G043900	40239993	40240628	-	response to stress
				TraesCS5A02G044100	40629011	40629322	+	response to stress
				TraesCS5A02G044200	40684638	40686436	+	response to stress
qYrS.43	5A	429474426	428974426-434474426	TraesCS5A02G213500	429169597	429173363	-	innate immune response, obsolete multi-organism process, defense response to bacterium, response to molecule of bacterial origin
				TraesCS5A02G213700	429476428	429477292	+	defense response
				TraesCS5A02G213900	29655586	429657535	-	response to bacterium, obsolete multi-organism process
				TraesCS5A02G214500	429986541	429990303	-	response to xenobiotic stimulus
				TraesCS5A02G215300	430637337	430643903	-	response to stress, response to stimulus
				TraesCS5A02G215900	432033398	432036973	-	response to fungus, response to stress
				TraesCS5A02G216300	433009341	433009541	+	response to stress
qYrS.44	5B	208728682	208228682-213728682	raesCS5B02G117800	208257701	208262499	+	response to stress
				TraesCS5B02G118200	208701414	208703518	+	defense response to fungu, obsolete multi-organism process
				TraesCS5B02G118600	209175783	209177206	-	response to stress
				TraesCS5B02G119500	211733944	211738654	+	response to stress
				TraesCS5B02G119600	211739093	211739284	-	response to stress

qYrS.45	5D	515407161	514907161- 520407161	TraesCS5D02G474800	514923266	514924170	-	response to stress
				TraesCS5D02G478200	517054084	517055294	+	immune response, positive regulation of immune response
				TraesCS5D02G478400	517213391	517214112	+	response to stress
				TraesCS5D02G479500	517600712	517605567	-	immune system process
				TraesCS5D02G480600	518787937	518798534	+	systemic acquired resistance
				TraesCS5D02G481700	519431831	519436380	-	response to stress, cellular response to endogenous stimulus
				TraesCS5D02G483000	520084228	520084833	-	defense response
				TraesCS5D02G483900	520347457	520348065	-	defense response to fungus, regulation of response to biotic stimulus, detection of biotic stimulus, plant-type hypersensitive response, negative regulation of defense response, defense response to bacterium,negative regulation of response to stimulus
qYrS.46	5D	529525683	529025683- 534525683	TraesCS5D02G501000	529256618	529258506	+	defense response to fungus, leaf senescence, response to oomycetes,
				TraesCS5D02G501100	529346790	529351653	+	regulation of defense response, systemic acquired resistance, obsolete multi- organism process
				TraesCS5D02G501800	529541894	529544315	-	systemic acquired resistance, obsolete multi-organism process
				TraesCS5D02G504300	530834635	530835459	+	defense response
				TraesCS5D02G508800	533912784	533914217	+	response to stimulus
				TraesCS5D02G508900	533999382	534003326	+	response to stress
qYrS.47	5D	533205336	532705336- 538205336	TraesCS5D02G508900	533999382	534003326	+	response to stress
				TraesCS5D02G508901	534090688	534095106	+	response to stress
				TraesCS5D02G510000	535005186	535008131	-	response to stress
				TraesCS5D02G511200	535916191	535922054	+	cellular response to stimulus

				TraesCS5D02G512400	536694355	536695158	+	defense response to bacterium, plant-type hypersensitive response
qYrS.48	6A	51769657	51269657-56769657	TraesCS6A02G082100	51373684	51374732	+	response to osmotic stress
				TraesCS6A02G082400	51406171	51409969	+	response to fungus
				TraesCS6A02G082900	51760523	51761891	+	response to osmotic stress, obsolete multi-organism process
				TraesCS6A02G083200	51948021	51953076	+	defense response to fungus, negative regulation of defense response, regulation of plant-type hypersensitive response,
				TraesCS6A02G083800	52287389	52289239	+	defense response to bacterium, obsolete regulation of multi-organism process, defense response to oomycetes
				TraesCS6A02G084400	53071982	53075458	+	defense response to fungus, regulation of defense response, defense response to bacterium, negative regulation of programmed cell death, obsolete multi-organism process
				TraesCS6A02G084900	53132997	53136394	+	defense response
				TraesCS6A02G085700	53910926	53911626	+	response to stress
				TraesCS6A02G086300	55013535	55014280	+	adaptive immune response based on somatic recombination of immune receptors built from immunoglobulin superfamily domains, immune effector process, positive regulation of response to stimulus, obsolete regulation of cell death, response to external stimulus
				TraesCS6A02G087000	55700360	55705297	+	response to stress
				TraesCS6A02G087900	56132883	56133110	-	response to stress
qYrS.49	6B	8235349	7735349-13235349	TraesCS6B02G013200	8372877	8375684	-	defense response, obsolete multi-organism process, response to other organism

				TraesCS6B02G013700	8416766	8420620	+	response to stimulus, ubiquitin-protein transferase activity, ubiquitin-protein transferase activity, protein ubiquitination, SCF-dependent proteasomal ubiquitin-dependent protein catabolic process
				TraesCS6B02G014400	8786252	8790077	-	response to fungus
				TraesCS6B02G014600	8888006	8889789	-	response to stress, ubiquitin-protein transferase activity, protein ubiquitination, SCF-dependent proteasomal ubiquitin-dependent protein catabolic process, SCF ubiquitin ligase complex,
				TraesCS6B02G016000	9759412	9759857	-	defense response to fungus
				TraesCS6B02G016500	10052204	10056776	+	defense response, response to biotic stimulus, obsolete multi-organism process
				TraesCS6B02G016700	10744852	10746514	-	defense response, response to biotic stimulus, obsolete multi-organism process
				TraesCS6B02G017900	11317464	11326092	-	MAPK cascade,
				TraesCS6B02G021300	12953761	12960319	+	defense response, response to biotic stimulus, ,
qYrS.50	6B	291067106	290567106-296067106	TraesCS6B02G214900	290627795	290629335	-	response to stimulus
				TraesCS6B02G215800	295765129	295769138	+	response to nematode, obsolete multi-organism process
qYrS.51	6B	476032032 - 583215607	471032032-588215607	TraesCS6B02G261000	470992398	471001839	-	response to bacterium
				TraesCS6B02G260700	470913286	470917399	-	response to bacterium, obsolete multi-organism process
				TraesCS6B02G260800	470918657	470921934	-	response to bacterium

				TraesCS6B02G261500	471232702	471235523	-	response to stimulus
				TraesCS6B02G261800	471506970	471510642	-	immune response, regulation of response to external stimulus
				TraesCS6B02G262100	472233975	472236545	+	response to stimulus
				TraesCS6B02G263700	474438130	474442077	-	response to stress
				TraesCS6B02G264600	476118839	476125138	+	defense response
				TraesCS6B02G265700	477791203	477793698	-	response to stimulus
				TraesCS6B02G266100	478470946	478480313	-	response to stress
				TraesCS6B02G328300	578209035	578213851	+	negative regulation of defense response, response to bacterium, response to virus
				TraesCS6B02G328400	578292778	578302379	+	response to virus, response to bacterium, regulation of plant-type hypersensitive response, negative regulation of defense response
				TraesCS6B02G328600	578396567	578406352	-	defense response to fungus, regulation of response to biotic stimulus, detection of biotic stimulus, plant-type hypersensitive response, negative regulation of defense response, defense response to bacterium, positive regulation of response to stimulus, obsolete multi-organism process, defense response by callose deposition, respiratory burst involved in defense response, regulation of response to biotic stimulus
				TraesCS6B02G329100	578525244	578525507	+	response to stress
				TraesCS6B02G330400	579549899	579550629	-	response to stress
				TraesCS6B02G331300	582391803	582401724	+	response to stimulus
				TraesCS6B02G331600	582865347	58286841	+	response to stimulus
qYrS.52	6B	664501564	664001564-669501564	TraesCS6B02G388800	664021498	664027063	-	defense response, obsolete multi-organism process, response to other organism

				TraesCS6B02G388900	664062456	664064312	-	defense response, defense response
				TraesCS6B02G389400	664256175	664267824	+	defense response to fungus, response to bacterium, systemic acquired resistance, negative regulation of defense response, obsolete multi-organism process
qYrS.53	6B	675702168	675202168-680702168	TraesCS6B02G400400	675792680	675793388	+	immune system process
				TraesCS6B02G400500	676036364	676037112	+	immune system process
				TraesCS6B02G400700	676123525	676124300	+	innate immune response, virus response
				TraesCS6B02G400800	676491787	676492725	-	immune system process
				TraesCS6B02G400900	676729858	676730736	-	immune system process
				TraesCS6B02G401000	676864930	676865881	-	immune system process, response to stress
				TraesCS6B02G401200	677087348	677088347	-	immune response, response to bacterium, obsolete multi-organism process
				TraesCS6B02G40200	678356927	678358254	+	immune system process, response to bacterium, obsolete multi-organism process
				TraesCS6B02G402300	678628031	678631004	+	defense response to fungus, obsolete multi-organism process
				TraesCS6B02G405200	680539973	680550188	-	defense response to insect, response to insect
qYrS.54	7A	12800907-50346076	7800907-55346076	TraesCS7A02G025400	10083381	10083869	+	immune response, response to stress, programmed cell death.,
				TraesCS7A02G025700	10168765	10169958	-	response to stress
				TraesCS7A02G026100	10357487	10358891	-	systemic acquired resistance, obsolete multi-organism process
				TraesCS7A02G026400	10619635	10626123	-	defense response, defense response, response to other organism
				TraesCS7A02G027600	11052777	11054056	-	response to stress
				TraesCS7A02G027700	11084872	11088792	+	defense response, response to biotic stimulus, obsolete multi-organism

								process
				TraesCS7A02G028300	11414317	11416000	+	defense response to fungus, obsolete multi-organism process, response to molecule of bacterial origin,
				TraesCS7A02G029200	11929896	11931329	+	cellular response to stress
				TraesCS7A02G031900	13189196	13192601	+	negative regulation of defense response
				TraesCS7A02G032100	13215430	13229260	-	defense response, response to other organism
				TraesCS7A02G031900	13189196	13192601	+	negative regulation of defense response
				TraesCS7A02G032200	13233387	13243208	+	defense response, obsolete multi-organism process, response to other organism
				TraesCS7A02G033900	14848028	14848561	-	immune response, obsolete regulation of cell death
				TraesCS7A02G034700	5274533	15276305	-	defense response to fungus, obsolete multi-organism process
				response to stress	15523755	15525871	-	response to stress
				TraesCS7A02G035100	15613759	15616374	+	response to stress, obsolete multi-organism process
				TraesCS7A02G035300	15688730	15689572	-	response to stress
				TraesCS7A02G037200	16669123	16696075	+	response to stress
				raesCS7A02G037700	16835876	16837161	-	defense response to fungus, regulation of response to biotic stimulus, regulation of plant-type hypersensitive response, negative regulation of defense response, defense response to bacterium, obsolete regulation of multi-organism process, obsolete regulation of multi-organism process, detection of biotic stimulus
				TraesCS7A02G037800	16876948	16877250	-	response to stress
				TraesCS7A02G039100	17439793	17444552	-	defense response, response to biotic stimulus, obsolete multi-organism

								process
				TraesCS7A02G039200	7466329	17467637	-	defense response, response to biotic stimulus
				TraesCS7A02G079500	45573584	45574047	-	defense response to fungus, killing of cells of another organism
				TraesCS7A02G080100	45980160	45982409	-	immune system process, response to stress
				TraesCS7A02G084300	48945918	48946997	-	defense response, obsolete multi-organism process, response to other organism
				TraesCS7A02G084400	49046290	49052241	-	response to molecule of fungal origin, response to molecule of bacterial origin, respiratory burst involved in defense response, detection of external stimulus,
				TraesCS7A02G086500	50575133	50575528	-	response to stress.
				TraesCS7A02G088300	53293391	53295206	-	defense response to bacterium
qYrS.55	7A	96563306-128909455	91563306-133909455	response to stress	94384012	94384399	-	response to stress
				TraesCS7A02G143200	94401050	94404595	-	regulation of defense response to virus
				TraesCS7A02G145900	97574642	97579612	-	defense response to bacterium, obsolete multi-organism process
				TraesCS7A02G146100	97873101	97873865	-	immune response
				TraesCS7A02G146100	98724764	98731773	+	response to stress
				TraesCS7A02G146800	99142323	99142541	-	response to stress, obsolete multi-organism process
				TraesCS7A02G147000	99674408	99677808	-	defense response, obsolete multi-organism process
				TraesCS7A02G147200	100063714	100064420	+	response to stress
				TraesCS7A02G169200	125992856	125994961	-	defense response, response to other organism
				TraesCS7A02G170400	126366120	126367643	-	response to stress
				TraesCS7A02G175200	128826237	128833021	+	MAPK cascade, systemic acquired

								resistance, salicylic acid mediated signaling pathway, regulation of plant-type hypersensitive response
qYrS.56	7A	730639307	730139307-735639307	TraesCS7A02G557700	730430495	730434493	-	defense response
				TraesCS7A02G557900	730504554	730505570	+	response to bacterium, obsolete multi-organism process
				TraesCS7A02G561200	732505046	732507142	+	defense response, response to biotic stimulusobsolete multi-organism process
				TraesCS7A02G561900	732919437	732923990	+	defense respons, response to biotic stimulusobsolete multi-organism process
				TraesCS7A02G562400	73321278	733220563	-	defense respons, response to biotic stimulusobsolete multi-organism process
qYrS.58	7D	353496936	352996936-358496936	TraesCS7D02G291600	351563387	351594278	-	negative regulation of defense response, regulation of plant-type hypersensitive response, response to stress
				TraesCS7D02G292500	358473307	358476106	+	response to stress

Supplementary table 8. GWAS complete output for agronomic traits. “Trait” indicates measured phenotypes, “AlleleID” reports allele identity, “Chr” indicates chromosomes (0 for unmapped). P.value” reports the significance of the nominal tests, “MAF” reports minor allele frequency. Highlighted markers are those significant at p value<0.05 threshold (-log(p value) of 3. HD= days to heading, FD= days to flowering, DM= days to maturity, TKW= thousand kernel weight, LA= leaf area, PH= plant height, SL= spike length, NSs= number of spikelets per spike, NKS= number of kernels per spike, NKSs= number of kernels per spikelets, SW= spike weight and GY=grain yield

Trait_Location	Allele ID	AlleleID	Chr	Position (bp)	P.value	maf	Nobs	Rsquare	Add effect	P.value (-log(p value))	Agronomic Trait
FD_Combined	1751	5971304 F 0-49:G>A-49:G>A	2B	733077296	0.00027571	0.18258427	178	0.137105848	-0.87331817	3.5595461	Days to flowering
FD_Combined	1916	1007086 F 0-41:C>T-41:C>T	2D	71621913	0.00031212	0.103932584	178	0.135950304	-1.18291507	3.50567769	Days to flowering
FD_Combined	1930	2245372 F 0-8:C>T-8:C>T	2D	78710021	0.00013824	0.199438202	178	0.143591004	-0.89514272	3.85936916	Days to flowering
FD_Combined	2369	1129265 F 0-9:C>T-9:C>T	3A	650045005	0.00032208	0.418539326	178	0.135646584	0.761724201	3.4920423	Days to flowering
FD_Combined	3630	1666326 F 0-11:T>C-11:T>C	4B	594693866	0.00048127	0.435393258	178	0.131872861	0.73611003	3.31760977	Days to flowering
FD_Combined	5352	1090345 F 0-8:T>A-8:T>A	6B	646747103	0.00052855	0.126404494	178	0.130993314	-1.0052619	3.27691263	Days to flowering
FD_Combined	5913	2293315 F 0-15:G>T-15:G>T	7A	636899963	0.00044307	0.143258427	178	0.132654424	-0.96266258	3.35352431	Days to flowering
FD_Combined	6696	1040763 F 0-30:G>A-30:G>A	7D	457185026	0.00092049	0.098314607	178	0.125777193	-1.07232293	3.03597887	Days to flowering
FD_Holeta	1869	1111954 F 0-51:A>G-51:A>G	2D	6710589	0.00029034	0.109550562	178	0.135003254	-1.48970796	3.53709791	Days to flowering
FD_Holeta	2369	1129265 F 0-9:C>T-9:C>T	3A	650045005	0.00071515	0.418539326	178	0.120246456	-1.24815565	3.14560034	Days to flowering
FD_Holeta	3630	1666326 F 0-11:T>C-11:T>C	4B	594693866	0.00074579	0.435393258	178	0.117763668	0.828322594	3.12738113	Days to flowering
FD_Holeta	5352	1090345 F 0-	6B	646747103	6.4901E-05	0.126404494	178	0.14702226	-1.34390219	4.18774872	Days to flowering

		8:T>A-8:T>A									
FD_Holeta	5353	1123012 F 0-16:G>C-16:G>C	6B	647836411	0.00095412	0.129213483	178	0.116658218	0.845163573	3.02039645	Days to flowering
FD_Holeta	5475	1124525 F 0-6:G>A-6:G>A	6D	12584252	0.00053097	0.120786517	178	0.124250102	-0.99906403	3.27493093	Days to flowering
FD_Kulumsa	1869	1111954 F 0-51:A>G-51:A>G	2D	6710589	0.00029034	0.109550562	178	0.135003254	-1.48970796	3.53709791	Days to flowering
FD_Kulumsa	2369	1129265 F 0-9:C>T-9:C>T	3A	650045005	0.00071515	0.418539326	178	0.120246456	-1.24815565	3.14560034	Days to flowering
FD_Kulumsa	3630	1666326 F 0-11:T>C-11:T>C	4B	594693866	0.00074579	0.435393258	178	0.117763668	0.828322594	3.12738113	Days to flowering
FD_Kulumsa	5352	1090345 F 0-8:T>A-8:T>A	6B	646747103	6.4901E-05	0.126404494	178	0.14702226	-1.34390219	4.18774872	Days to flowering
FD_Kulumsa	5353	1123012 F 0-16:G>C-16:G>C	6B	647836411	0.00095412	0.129213483	178	0.116658218	0.845163573	3.02039645	Days to flowering
FD_Kulumsa	5475	1124525 F 0-6:G>A-6:G>A	6D	12584252	0.00053097	0.120786517	178	0.124250102	-0.99906403	3.27493093	Days to flowering
FD_Meraro	939	1105748 F 0-62:C>G-62:C>G	2A	70983353	0.00089518	0.488764045	178	0.08274179	1.086141131	3.04808755	Days to flowering
FD_Meraro	1916	1007086 F 0-41:C>T-41:C>T	2D	71621913	0.00010841	0.103932584	178	0.100906246	-2.02833172	3.96493234	Days to flowering
FD_Meraro	2466	2261182 F 0-61:C>T-61:C>T	3A	728321059	0.00052274	0.126404494	178	0.087365288	1.651181017	3.28171262	Days to flowering
FD_Meraro	4178	1107504 F 0-28:T>G-28:T>G	5B	94270018	0.00050853	0.115168539	178	0.087604901	1.878195115	3.29368004	Days to flowering
GY_Combined	322	3020833 F 0-23:G>T-23:G>T	1B	57683566	0.00031213	0.148876404	178	0.136841906	-15.5067405	3.50566931	Grain yield
GY_Combined	454	1120791 F 0-30:A>G-30:A>G	1B	512632641	0.00024586	0.196629213	178	0.136858842	-23.0883393	3.60931129	Grain yield
GY_Combined	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.00022306	0.469101124	178	0.150455183	19.36504895	3.65158642	Grain yield
GY_Combined	943	5579629 F 0-18:G>A-18:G>A	2A	73179749	0.00049675	0.132022472	178	0.135228221	21.51503462	3.30386642	Grain yield
GY_Combined	2747	1694782 F 0-16:C>T-16:C>T	3B	630398506	0.00074417	0.216292135	178	0.129886694	-21.8485644	3.12833075	Grain yield

GY_Combined	5556	1220930 F 0-37:C>T-37:C>T	6D	456804572	0.00046091	0.112359551	178	0.135536071	-14.7797799	3.33638619	Grain yield
GY_Combined	6534	2246599 F 0-51:G>C-51:G>C	7D	14621383	0.00041027	0.47752809	178	0.136368108	-13.2381384	3.38693513	Grain yield
GY_Holeta	322	3020833 F 0-23:G>T-23:G>T	1B	57683566	0.00026643	0.148876404	178	0.141842438	34.67411733	3.57441132	Grain yield
GY_Holeta	454	1120791 F 0-30:A>G-30:A>G	1B	512632641	0.00027196	0.196629213	178	0.132719514	-22.7529587	3.56549758	Grain yield
GY_Holeta	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.00018152	0.469101124	178	0.161044076	31.74484644	3.74108576	Grain yield
GY_Holeta	943	5579629 F 0-18:G>A-18:G>A	2A	73179749	0.00043648	0.132022472	178	0.126913393	19.84531417	3.36003608	Grain yield
GY_Holeta	2747	1694782 F 0-16:C>T-16:C>T	3B	630398506	0.00072222	0.216292135	178	0.124354452	30.15229471	3.14133147	Grain yield
GY_Holeta	5556	1220930 F 0-37:C>T-37:C>T	6D	456804572	0.00049743	0.112359551	178	0.126532335	-30.1708189	3.30326472	Grain yield
GY_Holeta	6534	2246599 F 0-51:G>C-51:G>C	7D	14621383	0.00032168	0.47752809	178	0.130053602	20.91754412	3.49257344	Grain yield
GY_Kulumsa	343	1666581 F 0-9:T>C-9:T>C	1B	102154959	0.00025299	0.092696629	178	0.134808067	-23.8518662	3.5968883	Grain yield
GY_Kulumsa	899	989669 F 0-31:C>T-31:C>T	2A	28784582	0.00098177	0.418539326	178	0.097346713	8.907283779	3.00799122	Grain yield
GY_Kulumsa	2013	1092119 F 0-31:C>T-31:C>T	2D	478105342	0.00095897	0.129213483	178	0.123916083	-55.4218548	3.01819499	Grain yield
GY_Kulumsa	2073	2245811 F 0-7:T>C-7:T>C	2D	589243536	0.00070056	0.106741573	178	0.124631571	-33.3481089	3.15455241	Grain yield
GY_Kulumsa	2945	1229188 F 0-7:T>C-7:T>C	3D	951941	0.00042378	0.04494382	178	0.133291255	-28.1179065	3.37286362	Grain yield
GY_Kulumsa	3040	3937988 F 0-67:G>A-67:G>A	3D	349111387	0.00065724	0.08988764	178	0.132704184	-20.4654563	3.18227791	Grain yield
GY_Kulumsa	3384	1176591 F 0-59:A>G-59:A>G	4A	617850054	0.00021898	0.084269663	178	0.157509059	-42.0986314	3.65959398	Grain yield
GY_Meraro	343	1666581 F 0-9:T>C-9:T>C	1B	102154959	0.000253	0.092696629	178	0.089393734	3.596888301	3.5968883	Grain yield
GY_Meraro	899	989669 F 0-31:C>T-31:C>T	2A	28784582	0.00098177	0.418539326	178	0.080389262	3.007991216	3.00799122	Grain yield

GY_Meraro	2013	1092119 F 0-31:C>T-31:C>T	2D	478105342	0.00095897	0.129213483	178	0.080406503	3.018194989	3.01819499	Grain yield
GY_Meraro	2073	2245811 F 0-7:T>C-7:T>C	2D	589243536	0.00070056	0.106741573	178	0.081902158	3.154552411	3.15455241	Grain yield
GY_Meraro	2945	1229188 F 0-7:T>C-7:T>C	3D	951941	0.00042378	0.04494382	178	0.088031523	3.372863617	3.37286362	Grain yield
GY_Meraro	3040	3937988 F 0-67:G>A-67:G>A	3D	349111387	0.00065724	0.08988764	178	0.083381961	3.182277913	3.18227791	Grain yield
GY_Meraro	3384	1176591 F 0-59:A>G-59:A>G	4A	617850054	0.00021898	0.084269663	178	0.097346713	3.659593979	3.65959398	Grain yield
HD_Combined	27	1046200 F 0-9:T>C-9:T>C	1A	20893697	0.00016909	0.146067416	178	0.159638675	21.99048197	3.77187964	Heading date
HD_Combined	618	1113207 F 0-31:T>G-31:T>G	1B	641140613	0.00026791	0.415730337	178	0.131377066	11.49033791	3.57201739	Heading date
HD_Combined	1359	3025199 F 0-5:C>G-5:C>G	2B	30434696	0.00032615	0.132022472	178	0.105944975	14.10989941	3.48658844	Heading date
HD_Combined	1631	1125920 F 0-47:C>T-47:C>T	2B	602765799	0.00030645	0.421348315	178	0.109066771	14.6660139	3.51363438	Heading date
HD_Combined	2702	2251282 F 0-57:G>A-57:G>A	3B	562272656	0.00052919	0.148876404	178	0.10212445	10.1360287	3.27638617	Heading date
HD_Combined	4472	1257862 F 0-25:T>A-25:T>A	5B	631548275	0.00017793	0.255617978	178	0.143852549	15.0294201	3.74974821	Heading date
HD_Combined	4574	2293495 F 0-37:C>A-37:C>A	5D	99460869	0.00027562	0.123595506	178	0.129434435	13.87390932	3.55968369	Heading date
HD_Combined	4982	1018852 F 0-44:C>T-44:C>T	6A	582252775	0.00091471	0.112359551	178	0.095249473	8.442547195	3.03871522	Heading date
HD_Combined	5895	1222002 F 0-5:T>G-5:T>G	7A	621213334	0.00097099	0.134831461	178	0.093917691	7.333411197	3.01278573	Heading date
HD_Combined	5913	2293315 F 0-15:G>T-15:G>T	7A	636899963	0.00029835	0.143258427	178	0.116238173	16.93876546	3.52528101	Heading date
HD_Combined	5914	1382955 F 0-24:T>C-24:T>C	7A	636900029	4.5477E-05	0.050561798	178	0.17293515	17.9444106	4.34220993	Heading date
HD_Combined	6354	3222304 F 0-29:G>T-29:G>T	7B	630109864	0.00081877	0.191011236	178	0.095385375	9.189754787	3.08683822	Heading date
HD_Holeta	2702	2251282 F 0-57:G>A-57:G>A	3B	562272656	0.00013447	0.148876404	178	0.081563025	2.047585293	3.8713766	Heading date

HD_Holeta	5352	1090345 F 0-8:T>A-8:T>A	6B	646747103	0.00011011	0.126404494	178	0.100433946	3.549740879	3.95818752	Heading date
HD_Holeta	5353	1123012 F 0-16:G>C-16:G>C	6B	647836411	0.00054508	0.129213483	178	0.07416164	4.267580791	3.26353837	Heading date
HD_Kulumsa	27	1046200 F 0-9:T>C-9:T>C	1A	20893697	0.00091836	0.146067416	178	0.134589829	-1.75234457	3.03698538	Heading date
HD_Kulumsa	538	1139478 F 0-44:G>A-44:G>A	1B	585548359	0.00031927	0.483146067	178	0.141770368	-1.90835643	3.49584311	Heading date
HD_Kulumsa	1631	1125920 F 0-47:C>T-47:C>T	2B	602765799	0.00048587	0.421348315	178	0.136759026	1.79014721	3.31347888	Heading date
HD_Kulumsa	2344	2289202 F 0-36:T>A-36:T>A	3A	627917231	0.00028113	0.115168539	178	0.15077881	2.033559855	3.55109194	Heading date
HD_Kulumsa	3292	5324801 F 0-46:T>C-46:T>C	4A	143445913	0.00052933	0.078651685	178	0.136278751	-1.84667609	3.27627476	Heading date
HD_Kulumsa	4472	1257862 F 0-25:T>A-25:T>A	5B	631548275	0.00034295	0.255617978	178	0.137200761	-2.41649466	3.4647703	Heading date
HD_Kulumsa	5914	1382955 F 0-24:T>C-24:T>C	7A	636900029	0.00013454	0.050561798	178	0.162988188	-2.43776541	3.87116422	Heading date
HD_Meraro	623	1061145 F 0-36:A>G-36:A>G	1B	644598781	0.00043726	0.185393258	178	0.175061374	52.93949687	3.35926002	Heading date
HD_Meraro	4178	1107504 F 0-28:T>G-28:T>G	5B	94270018	0.00059335	0.115168539	178	0.158969653	64.18572793	3.22669028	Heading date
HD_Meraro	6270	1020753 F 0-10:C>T-10:C>T	7B	535230486	0.00091574	0.120786517	178	0.14957852	45.14459806	3.03822621	Heading date
LA_Combined	218	3064523 F 0-31:C>T-31:C>T	1A	556829236	0.00011481	0.050561798	178	0.129434435	13.87390932	3.9400162	Leaf area
LA_Combined	1535	1070207 F 0-37:T>C-37:T>C	2B	221486089	1.5051E-08	0.140449438	178	0.143852549	15.0294201	7.82243527	Leaf area
LA_Combined	2522	3937515 F 0-36:G>T-36:G>T	3B	9775233	0.00026808	0.058988764	178	0.116238173	16.93876546	3.57174013	Leaf area
LA_Combined	3697	1265768 F 0-44:T>C-44:T>C	4D	5662006	1.2648E-10	0.053370787	178	0.17293515	17.9444106	9.89797796	Leaf area
LA_Combined	4991	5371819 F 0-18:T>G-18:T>G	6A	586878964	1.1114E-08	0.047752809	178	0.159638675	21.99048197	7.95413647	Leaf area
LA_Combined	6265	4005310 F 0-58:T>C-58:T>C	7B	527961017	5.795E-07	0.058988764	178	0.131377066	11.49033791	6.2369465	Leaf area

LA_Holeta	774	1119123 F 0-11:C>G-11:C>G	1D	377576389	3.8589E-05	0.106741573	178	0.100433946	3.549740879	4.41353306	Leaf area
LA_Holeta	2456	2261182 F 0-61:C>T-61:C>T	3A	722465555	0.0002979	0.401685393	178	0.081563025	2.047585293	3.52593543	Leaf area
LA_Holeta	4181	5582198 F 0-11:G>A-11:G>A	5B	116830677	0.00066256	0.04494382	178	0.07416164	4.267580791	3.17877437	Leaf area
LA_Kulumsa	368	3034420 F 0-20:A>G-20:A>G	1B	336353718	0.0009132	0.185393258	178	0.136278751	-1.84667609	3.03943231	Leaf area
LA_Kulumsa	1000	2263493 F 0-26:G>A-26:G>A	2A	182570920	0.00083804	0.494382022	178	0.136759026	1.79014721	3.07673679	Leaf area
LA_Kulumsa	1042	1201430 F 0-58:G>A-58:G>A	2A	460327562	0.00097631	0.334269663	178	0.13278647	3.89030339	3.01041074	Leaf area
LA_Kulumsa	4662	2253187 F 0-50:G>A-50:G>A	5D	507377226	0.00064309	0.129213483	178	0.15077881	2.033559855	3.19172619	Leaf area
LA_Kulumsa	4786	1116192 F 0-11:A>G-11:A>G	6A	4666119	0.0007841	0.126404494	178	0.137200761	-2.41649466	3.10562839	Leaf area
LA_Kulumsa	5352	1090345 F 0-8:T>A-8:T>A	6B	646747103	0.00094855	0.126404494	178	0.134589829	-1.75234457	3.02293756	Leaf area
LA_Kulumsa	5719	999044 F 0-5:T>C-5:T>C	7A	81124905	2.9329E-08	0.188202247	178	0.162988188	-2.43776541	7.5327076	Leaf area
LA_Kulumsa	6450	7340828 F 0-11:C>G-11:C>G	7B	687056378	0.00064939	0.171348315	178	0.141770368	-1.90835643	3.18749158	Leaf area
LA_Meraro	218	3064523 F 0-31:C>T-31:C>T	1A	556829236	2.0196E-05	0.050561798	178	0.108771456	47.12462377	4.69473557	Leaf area
LA_Meraro	1535	1070207 F 0-37:T>C-37:T>C	2B	221486089	2.0536E-10	0.140449438	178	0.158969653	64.18572793	9.68748635	Leaf area
LA_Meraro	2086	5324627 F 0-45:G>C-45:G>C	2D	595557034	0.00024732	0.064606742	178	0.102119542	40.74037528	3.60673609	Leaf area
LA_Meraro	2522	3937515 F 0-36:G>T-36:G>T	3B	9775233	1.9305E-06	0.058988764	178	0.137784357	34.73984108	5.71433075	Leaf area
LA_Meraro	2547	6048363 F 0-45:A>G-45:A>G	3B	20554765	0.00020063	0.056179775	178	0.106335207	30.56930999	3.6975973	Leaf area
LA_Meraro	3697	1265768 F 0-44:T>C-44:T>C	4D	5662006	7.3037E-11	0.053370787	178	0.175061374	52.93949687	10.1364554	Leaf area
LA_Meraro	4991	5371819 F 0-18:T>G-18:T>G	6A	586878964	9.9115E-10	0.047752809	178	0.14957852	45.14459806	9.00386272	Leaf area

LA_Meraro	6265	4005310 F 0-58:T>C-58:T>C	7B	527961017	1.1154E-07	0.058988764	178	0.141061224	43.07124479	6.95258488	Leaf area
LA_Meraro	6567	3934789 F 0-19:G>A-19:G>A	7D	34137545	0.00094164	0.143258427	178	0.101306267	-1.52058271	3.02611679	Leaf area
LA_Meraro	6625	2374545 F 0-31:T>A-31:T>A	7D	86148750	0.00057644	0.081460674	178	0.101454	39.86647014	3.23924776	Leaf area
LA_Combined	218	3064523 F 0-31:C>T-31:C>T	1A	556829236	0.00011481	0.050561798	178	0.129434435	13.87390932	3.9400162	Leaf area
LA_Combined	1535	1070207 F 0-37:T>C-37:T>C	2B	221486089	1.5051E-08	0.140449438	178	0.143852549	15.0294201	7.82243527	Leaf area
LA_Combined	2522	3937515 F 0-36:G>T-36:G>T	3B	9775233	0.00026808	0.058988764	178	0.116238173	16.93876546	3.57174013	Leaf area
LA_Combined	3697	1265768 F 0-44:T>C-44:T>C	4D	5662006	1.2648E-10	0.053370787	178	0.17293515	17.9444106	9.89797796	Leaf area
LA_Combined	4991	5371819 F 0-18:T>G-18:T>G	6A	586878964	1.1114E-08	0.047752809	178	0.159638675	21.99048197	7.95413647	Leaf area
LA_Combined	6265	4005310 F 0-58:T>C-58:T>C	7B	527961017	5.795E-07	0.058988764	178	0.131377066	11.49033791	6.2369465	Leaf area
LA_Holeta	774	1119123 F 0-11:C>G-11:C>G	1D	377576389	3.8589E-05	0.106741573	178	0.100433946	3.549740879	4.41353306	Leaf area
LA_Holeta	2456	2261182 F 0-61:C>T-61:C>T	3A	722465555	0.0002979	0.401685393	178	0.081563025	2.047585293	3.52593543	Leaf area
LA_Holeta	4181	5582198 F 0-11:G>A-11:G>A	5B	116830677	0.00066256	0.04494382	178	0.07416164	4.267580791	3.17877437	Leaf area
LA_Kulumsa	368	3034420 F 0-20:A>G-20:A>G	1B	336353718	0.0009132	0.185393258	178	0.136278751	-1.84667609	3.03943231	Leaf area
LA_Kulumsa	1000	2263493 F 0-26:G>A-26:G>A	2A	182570920	0.00083804	0.494382022	178	0.136759026	1.79014721	3.07673679	Leaf area
LA_Kulumsa	1042	1201430 F 0-58:G>A-58:G>A	2A	460327562	0.00097631	0.334269663	178	0.13278647	3.89030339	3.01041074	Leaf area
LA_Kulumsa	4662	2253187 F 0-50:G>A-50:G>A	5D	507377226	0.00064309	0.129213483	178	0.15077881	2.033559855	3.19172619	Leaf area
LA_Kulumsa	4786	1116192 F 0-11:A>G-11:A>G	6A	4666119	0.0007841	0.126404494	178	0.137200761	-2.41649466	3.10562839	Leaf area
LA_Kulumsa	5352	1090345 F 0-8:T>A-8:T>A	6B	646747103	0.00094855	0.126404494	178	0.134589829	-1.75234457	3.02293756	Leaf area

LA_Kulumsa	5719	999044 F 0-5:T>C-5:T>C	7A	81124905	2.9329E-08	0.188202247	178	0.162988188	-2.43776541	7.5327076	Leaf area
LA_Kulumsa	6450	7340828 F 0-11:C>G-11:C>G	7B	687056378	0.00064939	0.171348315	178	0.141770368	-1.90835643	3.18749158	Leaf area
LA_Meraro	218	3064523 F 0-31:C>T-31:C>T	1A	556829236	2.0196E-05	0.050561798	178	0.108771456	47.12462377	4.69473557	Leaf area
LA_Meraro	1535	1070207 F 0-37:T>C-37:T>C	2B	221486089	2.0536E-10	0.140449438	178	0.158969653	64.18572793	9.68748635	Leaf area
LA_Meraro	2086	5324627 F 0-45:G>C-45:G>C	2D	595557034	0.00024732	0.064606742	178	0.102119542	40.74037528	3.60673609	Leaf area
LA_Meraro	2522	3937515 F 0-36:G>T-36:G>T	3B	9775233	1.9305E-06	0.058988764	178	0.137784357	34.73984108	5.71433075	Leaf area
LA_Meraro	2547	6048363 F 0-45:A>G-45:A>G	3B	20554765	0.00020063	0.056179775	178	0.106335207	30.56930999	3.6975973	Leaf area
LA_Meraro	3697	1265768 F 0-44:T>C-44:T>C	4D	5662006	7.3037E-11	0.053370787	178	0.175061374	52.93949687	10.1364554	Leaf area
LA_Meraro	4991	5371819 F 0-18:T>G-18:T>G	6A	586878964	9.9115E-10	0.047752809	178	0.14957852	45.14459806	9.00386272	Leaf area
LA_Meraro	6265	4005310 F 0-58:T>C-58:T>C	7B	527961017	1.1154E-07	0.058988764	178	0.141061224	43.07124479	6.95258488	Leaf area
LA_Meraro	6567	3934789 F 0-19:G>A-19:G>A	7D	34137545	0.00094164	0.143258427	178	0.101306267	-1.52058271	3.02611679	Leaf area
LA_Meraro	6625	2374545 F 0-31:T>A-31:T>A	7D	86148750	0.00057644	0.081460674	178	0.101454	39.86647014	3.23924776	Leaf area
MD_Combined	298	1244342 F 0-35:T>C-35:T>C	1B	20564759	0.00045732	0.452247191	178	0.079352417	0.84065845	3.33978438	Days to maturity
MD_Combined	1181	1077564 F 0-14:A>G-14:A>G	2A	734988239	0.00010151	0.126404494	178	0.092427452	-1.33131345	3.99349373	Days to maturity
MD_Combined	1501	3064537 F 0-50:C>T-50:C>T	2B	164642274	0.00091863	0.384831461	178	0.074008297	0.836829935	3.03685839	Days to maturity
MD_Combined	1647	991531 F 0-13:A>C-13:A>C	2B	638230965	0.00021802	0.365168539	178	0.083110893	-0.95045448	3.66149481	Days to maturity
MD_Combined	2336	3023149 F 0-12:T>G-12:T>G	3A	621586722	0.00040587	0.146067416	178	0.082465757	-1.04994564	3.39161651	Days to maturity
MD_Combined	2338	2264298 F 0-16:C>T-16:C>T	3A	624928879	0.00043472	0.053370787	178	0.079815784	0.794424746	3.36179533	Days to maturity

MD_Combined	4495	4909394 F 0-9:A>G-9:A>G	5B	665027137	0.00073508	0.04494382	178	0.077156709	-1.32167779	3.13366486	Days to maturity
MD_Combined	4730	2242904 F 0-17:T>C-17:T>C	5D	542992656	0.00051566	0.095505618	178	0.079185393	-0.87922365	3.28763868	Days to maturity
MD_Holeta	88	4405667 F 0-32:T>C-32:T>C	1A	432956709	3.2099E-08	0.050561798	178	0.107129656	-4.42920276	7.49350801	Days to maturity
MD_Holeta	91	989749 F 0-20:C>T-20:C>T	1A	443168524	0.00065336	0.16011236	178	0.077377836	-3.4100937	3.18485062	Days to maturity
MD_Holeta	117	2262966 F 0-47:A>C-47:A>C	1A	481771181	0.00053516	0.373595506	178	0.080727375	-3.96396835	3.27151863	Days to maturity
MD_Holeta	119	2259122 F 0-62:A>C-62:A>C	1A	484300587	0.00019492	0.376404494	178	0.081781703	-3.21772734	3.71014064	Days to maturity
MD_Holeta	329	3025893 F 0-28:A>G-28:A>G	1B	67020984	0.00065896	0.193820225	178	0.076364785	-2.44779484	3.18114228	Days to maturity
MD_Holeta	2568	1234768 F 0-5:T>C-5:T>C	3B	24929087	2.7889E-06	0.154494382	178	0.089015836	-2.75381122	5.55456781	Days to maturity
MD_Holeta	3749	1240203 F 0-56:C>T-56:C>T	5A	4208674	8.6423E-06	0.132022472	178	0.083230456	-3.37669857	5.06337003	Days to maturity
MD_Holeta	4354	1114619 F 0-46:T>G-46:T>G	5B	526838601	0.00096319	0.320224719	178	0.074885479	-3.25446927	3.01628955	Days to maturity
MD_Holeta	4495	4909394 F 0-9:A>G-9:A>G	5B	665027137	7.4861E-06	0.04494382	178	0.08592731	-4.02429257	5.12574312	Days to maturity
MD_Kulumsa	298	1244342 F 0-35:T>C-35:T>C	1B	20564759	0.00041742	0.452247191	178	0.068689341	1.476055721	3.37942561	Days to maturity
MD_Kulumsa	480	991389 F 0-29:C>T-29:C>T	1B	533096804	0.00041769	0.06741573	178	0.067185485	1.382436057	3.37914193	Days to maturity
MD_Kulumsa	708	1019670 F 0-36:G>A-36:G>A	1D	29838843	0.00084783	0.196629213	178	0.064776867	-1.64137768	3.0716907	Days to maturity
MD_Kulumsa	2120	3064574 F 0-36:G>A-36:G>A	2D	613018750	0.00030905	0.334269663	178	0.081550609	-2.39425008	3.50997674	Days to maturity
MD_Kulumsa	2344	2289202 F 0-36:T>A-36:T>A	3A	627917231	0.00018182	0.115168539	178	0.08195258	-1.94507687	3.74035633	Days to maturity
MD_Kulumsa	2879	4910275 F 0-52:T>C-52:T>C	3B	780625758	0.00073968	0.04494382	178	0.065167802	1.496813622	3.13095513	Days to maturity
MD_Kulumsa	3506	2265458 F 0-29:T>C-29:T>C	4B	7463286	0.00050322	0.401685393	178	0.065344768	-2.80243674	3.29823847	Days to maturity

MD_Kulumsa	4395	2258883 F 0-54:G>T-54:G>T	5B	541284213	0.00098267	0.162921348	178	0.063583799	-1.86232166	3.00759356	Days to maturity
MD_Kulumsa	5763	993598 F 0-68:T>G-68:T>G	7A	126777072	0.00016253	0.117977528	178	0.087598535	-2.55658927	3.78905972	Days to maturity
MD_Meraro	631	2278863 F 0-40:G>A-40:G>A	1B	648792411	0.00066912	0.039325843	178	0.085825964	0.727381353	3.17449532	Days to maturity
MD_Meraro	939	1105748 F 0-62:C>G-62:C>G	2A	70983353	0.00085025	0.488764045	178	0.084939629	0.877063847	3.07045404	Days to maturity
MD_Meraro	1309	1097808 F 0-60:G>A-60:G>A	2B	2522696	0.00043814	0.129213483	178	0.09160281	1.249905074	3.3583864	Days to maturity
MD_Meraro	3449	1312192 F 0-10:G>T-10:G>T	4A	700728477	0.00066468	0.45505618	178	0.086373611	-1.61025947	3.17738716	Days to maturity
MD_Meraro	4627	1087971 F 0-29:A>T-29:A>T	5D	421238147	0.00049144	0.146067416	178	0.091353972	-1.36320316	3.30853076	Days to maturity
MD_Meraro	4731	1218555 F 0-50:G>A-50:G>A	5D	543072796	0.00083762	0.297752809	178	0.08581133	0.816769271	3.07695548	Days to maturity
MD_Meraro	4877	1694710 F 0-62:G>C-62:G>C	6A	83260267	0.00061779	0.058988764	178	0.087281034	-0.80798778	3.2091576	Days to maturity
MD_Meraro	5408	2261198 F 0-23:C>G-23:C>G	6B	698048660	0.00054457	0.20505618	178	0.088159886	1.542839154	3.26394428	Days to maturity
NKS_Combined	582	1042822 F 0-20:G>A-20:G>A	1B	622709384	1.9204E-05	0.137640449	178	0.125537759	0.731454563	4.71660275	Number of kernels per spike
NKS_Combined	818	991540 F 0-50:A>G-50:A>G	1D	426925916	0.000535	0.143258427	178	0.117830476	0.727476079	3.27164329	Number of kernels per spike
NKS_Combined	1319	1105975 F 0-49:C>T-49:C>T	2B	13755354	0.00084116	0.379213483	178	0.112581567	0.658698182	3.0751205	Number of kernels per spike
NKS_Combined	1519	1104343 F 0-56:A>G-56:A>G	2B	197708090	3.4293E-06	0.123595506	178	0.126700265	0.671718206	5.46479454	Number of kernels per spike
NKS_Combined	1756	2282050 F 0-28:C>G-28:C>G	2B	734672774	1.7747E-05	0.084269663	178	0.125869077	0.651253111	4.75087371	Number of kernels per spike
NKS_Combined	2271	992022 F 0-9:G>A-9:G>A	3A	222047569	2.516E-06	0.098314607	178	0.136422712	0.730316081	5.59928603	Number of kernels per spike
NKS_Combined	3161	997084 F 0-7:C>T-7:C>T	3D	590041455	0.00041981	0.129213483	178	0.119492886	0.575408742	3.37694523	Number of kernels per spike
NKS_Combined	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	1.9806E-06	0.137640449	178	0.137208353	0.697923125	5.70319456	Number of kernels per spike

NKS_Combined	5109	1074980 F 0-42:G>A-42:G>A	6B	35516182	0.00075315	0.140449438	178	0.112830104	0.586137851	3.12312073	Number of kernels per spike
NKS_Combined	5538	2244423 F 0-18:C>T-18:C>T	6D	406620794	0.00063132	0.143258427	178	0.115898049	0.747957092	3.19975088	Number of kernels per spike
NKS_Combined	5740	3029599 F 0-13:C>T-13:C>T	7A	94404278	0.00093726	0.081460674	178	0.110472073	1.003883499	3.02813892	Number of kernels per spike
NKS_Holeta	112	1099971 F 0-31:C>T-31:C>T	1A	480934139	0.00099155	0.308988764	178	0.156390747	2.086538464	3.00368531	Number of kernels per spike
NKS_Holeta	582	1042822 F 0-20:G>A-20:G>A	1B	622709384	4.5013E-06	0.137640449	178	0.163071881	2.16027434	5.34665859	Number of kernels per spike
NKS_Holeta	1520	1126316 F 0-23:A>G-23:A>G	2B	198011408	1.4346E-08	0.123595506	178	0.191705315	2.268673961	7.84326446	Number of kernels per spike
NKS_Holeta	1756	2282050 F 0-28:C>G-28:C>G	2B	734672774	0.00091666	0.084269663	178	0.15662781	3.012624369	3.03779389	Number of kernels per spike
NKS_Holeta	2128	998651 F 0-24:G>C-24:G>C	2D	615503378	0.00071996	0.353932584	178	0.159192773	2.193017481	3.14268941	Number of kernels per spike
NKS_Holeta	2271	992022 F 0-9:G>A-9:G>A	3A	222047569	8.4676E-07	0.098314607	178	0.166728771	1.856943797	6.0722386	Number of kernels per spike
NKS_Holeta	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	2.7689E-07	0.137640449	178	0.166792143	1.876523872	6.55769163	Number of kernels per spike
NKS_Holeta	5729	1118816 F 0-9:T>C-9:T>C	7A	85601206	6.3027E-06	0.151685393	178	0.161979713	1.819197217	5.20047344	Number of kernels per spike
NKS_Holeta	6515	1068599 F 0-31:A>G-31:A>G	7D	6137281	0.00072716	0.168539326	178	0.158647437	1.821524644	3.13837295	Number of kernels per spike
NKS_Kulumsa	1445	1696684 F 0-6:A>G-6:A>G	2B	104940392	0.00099898	0.320224719	178	0.065055066	0.15443431	3.00044529	Number of kernels per spike
NKS_Kulumsa	1446	1128199 F 0-47:A>G-47:A>G	2B	104940458	0.00044684	0.331460674	178	0.072920564	0.164022924	3.34984829	Number of kernels per spike
NKS_Kulumsa	2720	1064277 F 0-35:C>T-35:C>T	3B	586142000	0.0006692	0.146067416	178	0.068970624	-0.18257408	3.17444103	Number of kernels per spike
NKS_Kulumsa	2805	2295854 F 0-22:C>G-22:C>G	3B	728922365	0.00025393	0.216292135	178	0.078445136	0.188667771	3.59527889	Number of kernels per spike
NKS_Meraro	1138	1022408 F 0-63:G>C-63:G>C	2A	708156038	1.0166E-07	0.06741573	178	0.125199304	0.519312909	6.99283727	Number of kernels per spike
NKS_Meraro	1197	2255667 F 0-41:C>G-41:C>G	2A	744286377	0.00067382	0.162921348	178	0.085012283	0.268521179	3.171458	Number of kernels per spike

NKS_Meraro	1587	1212973 F 0-21:A>G-21:A>G	2B	477157264	0.00078047	0.216292135	178	0.072845265	-0.19177206	3.10764469	Number of kernels per spike
NKS_Meraro	2975	1205259 F 0-50:G>T-50:G>T	3D	29861477	0.00072524	0.137640449	178	0.077249282	0.195070713	3.13952061	Number of kernels per spike
NKS_Meraro	3741	1162593 F 0-10:T>C-10:T>C	4D	506496385	0.00053387	0.103932584	178	0.10485938	0.267932329	3.27256478	Number of kernels per spike
NKSs_Combined	1468	2325438 F 0-27:A>G-27:A>G	2B	122267367	0.0001889	0.126404494	178	0.171170051	0.565359613	3.72375896	Number of kernels per spikelets
NKSs_Combined	1511	1042631 F 0-26:G>C-26:G>C	2B	184494452	0.00052758	0.112359551	178	0.170062691	0.600117119	3.27771402	Number of kernels per spikelets
NKSs_Combined	1612	1090446 F 0-21:T>C-21:T>C	2B	573722860	1.5977E-07	0.146067416	178	0.180047516	0.68254176	6.7965089	Number of kernels per spikelets
NKSs_Combined	2625	1218511 F 0-55:T>C-55:T>C	3B	82624614	2.1953E-05	0.098314607	178	0.17390722	0.551149428	4.65850168	Number of kernels per spikelets
NKSs_Combined	2819	1035788 F 0-50:G>T-50:G>T	3B	738156443	0.00078683	0.311797753	178	0.167737322	0.733105888	3.10412181	Number of kernels per spikelets
NKSs_Combined	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	1.4521E-05	0.137640449	178	0.174216303	0.702640974	4.83801225	Number of kernels per spikelets
NKSs_Combined	5538	2244423 F 0-18:C>T-18:C>T	6D	406620794	7.5286E-06	0.143258427	178	0.174361792	0.625468311	5.12328444	Number of kernels per spikelets
NKSs_Combined	5666	1073357 F 0-18:A>C-18:A>C	7A	38241544	0.00096724	0.165730337	178	0.166213879	0.694624868	3.01446519	Number of kernels per spikelets
NKSs_Combined	5667	1266301 F 0-16:T>C-16:T>C	7A	38327804	0.0008657	0.112359551	178	0.16623308	0.55491333	3.06263179	Number of kernels per spikelets
NKSs_Combined	6419	1246695 F 0-6:T>C-6:T>C	7B	672400921	0.00045913	0.140449438	178	0.170290711	0.548178006	3.33806785	Number of kernels per spikelets
NKSs_Combined	6724	1047128 F 0-13:T>G-13:T>G	7D	548916083	3.011E-06	0.370786517	178	0.179144374	0.64503487	5.52128826	Number of kernels per spikelets
NKSs_Holeta	629	1268498 F 0-6:T>C-6:T>C	1B	646476073	0.00039957	0.050561798	178	0.096199305	0.404212219	3.39841075	Number of kernels per spikelets
NKSs_Holeta	1625	1211331 F 0-16:A>C-16:A>C	2B	598559595	3.4053E-07	0.491573034	178	0.112921349	0.30894273	6.46784221	Number of kernels per spikelets
NKSs_Holeta	2716	4993252 F 0-60:G>T-60:G>T	3B	581975772	1.4809E-06	0.04494382	178	0.109776931	0.395832388	5.82947948	Number of kernels per spikelets
NKSs_Holeta	5890	4993223 F 0-12:A>G-12:A>G	7A	614780849	0.00059288	0.08988764	178	0.095274064	0.300885966	3.22703582	Number of kernels per spikelets

NKSs_Holeta	5932	1031455 F 0-32:C>A-32:C>A	7A	652721642	0.00072697	0.258426966	178	0.094866826	0.312732927	3.13848335	Number of kernels per spikelets
NKSs_Holeta	6209	1388220 F 0-20:G>C-20:G>C	7B	302413910	4.0903E-12	0.033707865	178	0.143978108	0.686139522	11.3882412	Number of kernels per spikelets
NKSs_Holeta	6247	1046551 F 0-43:A>T-43:A>T	7B	481660548	0.00075043	0.109550562	178	0.094358752	0.344913791	3.12469065	Number of kernels per spikelets
NKSs_Holeta	6576	1012066 F 0-21:C>A-21:C>A	7D	42519818	5.3233E-06	0.075842697	178	0.098687871	0.361890837	5.27381608	Number of kernels per spikelets
NKSs_Kulumsa	283	1057381 F 0-34:T>C-34:T>C	1B	7160074	0.00091394	0.095505618	178	0.070154655	0.291104283	3.03908314	Number of kernels per spikelets
NKSs_Kulumsa	511	1081747 F 0-27:T>C-27:T>C	1B	565566678	0.000945	0.235955056	178	0.067518057	0.301625637	3.02456966	Number of kernels per spikelets
NKSs_Kulumsa	1293	993911 F 0-34:T>A-34:T>A	2A	773513489	5.2729E-06	0.092696629	178	0.091745192	0.474713068	5.27795296	Number of kernels per spikelets
NKSs_Kulumsa	2950	5324914 F 0-25:C>G-25:C>G	3D	9292491	0.00075046	0.126404494	178	0.076189371	0.371777454	3.12466994	Number of kernels per spikelets
NKSs_Kulumsa	4025	994426 F 0-56:C>A-56:C>A	5A	613471746	2.5718E-12	0.039325843	178	0.130383898	0.557653929	11.5897567	Number of kernels per spikelets
NKSs_Kulumsa	4749	1250261 F 0-56:G>T-56:G>T	5D	549647903	0.00020176	0.098314607	178	0.086258705	0.334020155	3.69517527	Number of kernels per spikelets
NKSs_Kulumsa	5021	1254459 F 0-8:A>C-8:A>C	6A	602989232	6.3918E-05	0.412921348	178	0.089719166	0.386187485	4.19437369	Number of kernels per spikelets
NKSs_Kulumsa	6213	1063747 F 0-8:C>T-8:C>T	7B	328548376	5.0209E-06	0.058988764	178	0.099141352	0.460700893	5.29922187	Number of kernels per spikelets
NKSs_Meraro	582	1042822 F 0-20:G>A-20:G>A	1B	622709384	4.4493E-06	0.137640449	178	0.162543464	2.148829106	5.35170843	Number of kernels per spikelets
NKSs_Meraro	1520	1126316 F 0-23:A>G-23:A>G	2B	198011408	1.4004E-08	0.123595506	178	0.191425256	2.262438808	7.85373838	Number of kernels per spikelets
NKSs_Meraro	1756	2282050 F 0-28:C>G-28:C>G	2B	734672774	0.00092704	0.084269663	178	0.157151396	1.973190953	3.0329012	Number of kernels per spikelets
NKSs_Meraro	2128	998651 F 0-24:G>C-24:G>C	2D	615503378	0.0006481	0.353932584	178	0.160938532	1.848026318	3.18836071	Number of kernels per spikelets
NKSs_Meraro	2271	992022 F 0-9:G>A-9:G>A	3A	222047569	8.8009E-07	0.098314607	178	0.1664256	1.868973809	6.05547117	Number of kernels per spikelets
NKSs_Meraro	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	2.2508E-07	0.137640449	178	0.166692144	1.853419519	6.64767039	Number of kernels per spikelets

NKSs_Meraro	5729	1118816 F 0-9:T>C-9:T>C	7A	85601206	6.1768E-06	0.151685393	178	0.162395946	1.821227307	5.20923979	Number of kernels per spikelets
NKSs_Meraro	6515	1068599 F 0-31:A>G-31:A>G	7D	6137281	0.00075088	0.168539326	178	0.159164542	2.188660497	3.12442774	Number of kernels per spikelets
NSsS_Combined	1468	2325438 F 0-27:A>G-27:A>G	2B	122267367	0.0001889	0.126404494	178	0.06862684	0.412727064	3.72375896	Number of spikelets per spike
NSsS_Combined	1511	1042631 F 0-26:G>C-26:G>C	2B	184494452	0.00052758	0.112359551	178	0.065242855	-0.2866375	3.27771402	Number of spikelets per spike
NSsS_Combined	1612	1090446 F 0-21:T>C-21:T>C	2B	573722860	1.5977E-07	0.146067416	178	0.106375115	0.650035454	6.7965089	Number of spikelets per spike
NSsS_Combined	2625	1218511 F 0-55:T>C-55:T>C	3B	82624614	2.1953E-05	0.098314607	178	0.070681239	-0.28159111	4.65850168	Number of spikelets per spike
NSsS_Combined	2819	1035788 F 0-50:G>T-50:G>T	3B	738156443	0.00078683	0.311797753	178	0.06502911	0.564472385	3.10412181	Number of spikelets per spike
NSsS_Combined	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	1.4521E-05	0.137640449	178	0.072769981	-0.31848796	4.83801225	Number of spikelets per spike
NSsS_Combined	5538	2244423 F 0-18:C>T-18:C>T	6D	406620794	7.5286E-06	0.143258427	178	0.091750721	-0.34001573	5.12328444	Number of spikelets per spike
NSsS_Combined	5666	1073357 F 0-18:A>C-18:A>C	7A	38241544	0.00096724	0.165730337	178	0.06185635	0.486980683	3.01446519	Number of spikelets per spike
NSsS_Combined	5667	1266301 F 0-16:T>C-16:T>C	7A	38327804	0.0008657	0.112359551	178	0.064658151	0.305391362	3.06263179	Number of spikelets per spike
NSsS_Combined	6419	1246695 F 0-6:T>C-6:T>C	7B	672400921	0.00045913	0.140449438	178	0.068028113	-0.30692634	3.33806785	Number of spikelets per spike
NSsS_Combined	6724	1047128 F 0-13:T>G-13:T>G	7D	548916083	3.011E-06	0.370786517	178	0.105322505	0.784850651	5.52128826	Number of spikelets per spike
NSsS_Holeta	629	1268498 F 0-6:T>C-6:T>C	1B	646476073	0.00039957	0.050561798	178	0.06370401	0.647596587	3.39841075	Number of spikelets per spike
NSsS_Holeta	1625	1211331 F 0-16:A>C-16:A>C	2B	598559595	3.4053E-07	0.491573034	178	0.075254125	0.717911397	6.46784221	Number of spikelets per spike
NSsS_Holeta	2716	4993252 F 0-60:G>T-60:G>T	3B	581975772	1.4809E-06	0.04494382	178	0.074204134	0.833712363	5.82947948	Number of spikelets per spike
NSsS_Holeta	5890	4993223 F 0-12:A>G-12:A>G	7A	614780849	0.00059288	0.08988764	178	0.060783096	0.487094756	3.22703582	Number of spikelets per spike
NSsS_Holeta	5932	1031455 F 0-32:C>A-32:C>A	7A	652721642	0.00072697	0.258426966	178	0.058737697	0.618597395	3.13848335	Number of spikelets per spike

NSsS_Holeta	6209	1388220 F 0-20:G>C-20:G>C	7B	302413910	4.0903E-12	0.033707865	178	0.077951895	0.768117036	11.3882412	Number of spikelets per spike
NSsS_Holeta	6247	1046551 F 0-43:A>T-43:A>T	7B	481660548	0.00075043	0.109550562	178	0.057262244	0.68782239	3.12469065	Number of spikelets per spike
NSsS_Holeta	6576	1012066 F 0-21:C>A-21:C>A	7D	42519818	5.3233E-06	0.075842697	178	0.064703638	0.799818964	5.27381608	Number of spikelets per spike
NSsS_Kulumsa	283	1057381 F 0-34:T>C-34:T>C	1B	7160074	0.00091394	0.095505618	178	0.08640249	0.764293552	3.03908314	Number of spikelets per spike
NSsS_Kulumsa	511	1081747 F 0-27:T>C-27:T>C	1B	565566678	0.000945	0.235955056	178	0.082140105	-0.56490496	3.02456966	Number of spikelets per spike
NSsS_Kulumsa	1293	993911 F 0-34:T>A-34:T>A	2A	773513489	5.2729E-06	0.092696629	178	0.103402051	0.84491564	5.27795296	Number of spikelets per spike
NSsS_Kulumsa	2950	5324914 F 0-25:C>G-25:C>G	3D	9292491	0.00075046	0.126404494	178	0.087129604	0.803803024	3.12466994	Number of spikelets per spike
NSsS_Kulumsa	4025	994426 F 0-56:C>A-56:C>A	5A	613471746	2.5718E-12	0.039325843	178	0.154193261	1.195554224	11.5897567	Number of spikelets per spike
NSsS_Kulumsa	4749	1250261 F 0-56:G>T-56:G>T	5D	549647903	0.00020176	0.098314607	178	0.091187536	0.642879956	3.69517527	Number of spikelets per spike
NSsS_Kulumsa	5021	1254459 F 0-8:A>C-8:A>C	6A	602989232	6.3918E-05	0.412921348	178	0.09294812	1.011680136	4.19437369	Number of spikelets per spike
NSsS_Kulumsa	6213	1063747 F 0-8:C>T-8:C>T	7B	328548376	5.0209E-06	0.058988764	178	0.116057066	1.062598282	5.29922187	Number of spikelets per spike
NSsS_Meraro	582	1042822 F 0-20:G>A-20:G>A	1B	622709384	4.4493E-06	0.137640449	178	0.100606569	0.517835372	5.35170843	Number of spikelets per spike
NSsS_Meraro	1520	1126316 F 0-23:A>G-23:A>G	2B	198011408	1.4004E-08	0.123595506	178	0.111666988	0.738388915	7.85373838	Number of spikelets per spike
NSsS_Meraro	1756	2282050 F 0-28:C>G-28:C>G	2B	734672774	0.00092704	0.084269663	178	0.086674885	-0.47675647	3.0329012	Number of spikelets per spike
NSsS_Meraro	2128	998651 F 0-24:G>C-24:G>C	2D	615503378	0.0006481	0.353932584	178	0.0959781	-0.46362421	3.18836071	Number of spikelets per spike
NSsS_Meraro	2271	992022 F 0-9:G>A-9:G>A	3A	222047569	8.8009E-07	0.098314607	178	0.102382824	0.502755467	6.05547117	Number of spikelets per spike
NSsS_Meraro	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	2.2508E-07	0.137640449	178	0.108426486	-0.54281894	6.64767039	Number of spikelets per spike
NSsS_Meraro	5729	1118816 F 0-9:T>C-9:T>C	7A	85601206	6.1768E-06	0.151685393	178	0.099491185	0.478041143	5.20923979	Number of spikelets per spike

NSsS_Meraro	6515	1068599 F 0-31:A>G-31:A>G	7D	6137281	0.00075088	0.168539326	178	0.091522496	0.613901806	3.12442774	Number of spikelets per spike
PH_Combined	1166	1006861 F 0-50:G>C-50:G>C	2A	723358962	8.7457E-05	0.179775281	178	0.100307384	1.803251974	4.05820424	Plant height
PH_Combined	1468	2325438 F 0-27:A>G-27:A>G	2B	122267367	0.0001889	0.126404494	178	0.067557948	1.862664915	3.72375896	Plant height
PH_Combined	1511	1042631 F 0-26:G>C-26:G>C	2B	184494452	0.00052758	0.112359551	178	0.066180621	-1.09049626	3.27771402	Plant height
PH_Combined	1612	1090446 F 0-21:T>C-21:T>C	2B	573722860	0.00000016	0.146067416	178	0.07210878	-1.20005687	6.7965089	Plant height
PH_Combined	2625	1218511 F 0-55:T>C-55:T>C	3B	82624614	0.000022	0.098314607	178	0.06783709	1.724288966	4.65850168	Plant height
PH_Combined	2819	1035788 F 0-50:G>T-50:G>T	3B	738156443	0.00078683	0.311797753	178	0.065758492	-1.10978153	3.10412181	Plant height
PH_Combined	3377	1233192 F 0-29:C>T-29:C>T	4A	612662292	0.0000145	0.137640449	178	0.07043955	2.032544086	4.83801225	Plant height
PH_Combined	5538	2244423 F 0-18:C>T-18:C>T	6D	406620794	0.00000753	0.143258427	178	0.071021928	2.84341228	5.12328444	Plant height
PH_Combined	5666	1073357 F 0-18:A>C-18:A>C	7A	38241544	0.00096724	0.165730337	178	0.062743722	1.777671339	3.01446519	Plant height
PH_Combined	5667	1266301 F 0-16:T>C-16:T>C	7A	38327804	0.0008657	0.112359551	178	0.064089014	-1.16908713	3.06263179	Plant height
PH_Combined	6419	1246695 F 0-6:T>C-6:T>C	7B	672400921	0.00045913	0.140449438	178	0.067075411	1.064610087	3.33806785	Plant height
PH_Combined	6724	1047128 F 0-	7D	548916083	0.00000301	0.370786517	178	0.071756204	1.373432287	5.52128826	Plant height

		13:T>G-13:T>G									
PH_Holeta	894	1088511 F 0-7:T>C-7:T>C	2A	16730048	0.00033232	0.474719101	178	0.074925476	1.543835484	3.47843749	Plant height
PH_Holeta	1315	1262031 F 0-29:G>A-29:G>A	2B	9283046	0.00064568	0.43258427	178	0.066396082	1.496680845	3.18998093	Plant height
PH_Holeta	1873	1215097 F 0-65:G>A-65:G>A	2D	15732248	0.00063664	0.497191011	178	0.066660733	-2.85672394	3.19610531	Plant height
PH_Holeta	5325	1141272 F 0-22:T>A-22:T>A	6B	631137282	0.000353	0.463483146	178	0.074253106	-1.49612801	3.45223007	Plant height
PH_Holeta	5326	4911043 F 0-44:C>T-44:C>T	6B	631138252	4.9688E-05	0.401685393	178	0.09583036	-1.66376498	4.30375219	Plant height
PH_Kulumsa	1166	1006861 F 0-50:G>C-50:G>C	2A	723358962	0.0005004	0.179775281	178	0.098383952	2.26788618	3.30068162	Plant height
PH_Kulumsa	3257	1110860 F 0-43:T>C-43:T>C	4A	22219271	0.00091094	0.129213483	178	0.092200193	2.282934384	3.04050875	Plant height
PH_Kulumsa	4212	1047582 F 0-52:C>G-52:C>G	5B	327196367	0.00037785	0.078651685	178	0.100821203	-3.66008862	3.4226759	Plant height
PH_Meraro	791	1215797 F 0-17:G>T-17:G>T	1D	414719500	0.00059817	0.087078652	178	0.082865172	2.431063665	3.22317339	Plant height
PH_Meraro	1501	3064537 F 0-50:C>T-50:C>T	2B	164642274	0.00070941	0.384831461	178	0.076334373	1.888249338	3.14910571	Plant height
PH_Meraro	3290	1080439 F 0-41:A>G-41:A>G	4A	140700686	0.00050748	0.146067416	178	0.099147346	3.595535752	3.29458283	Plant height
PH_Meraro	3339	3025953 F 0-25:G>A-25:G>A	4A	521603853	0.00090081	0.16011236	178	0.066298173	2.534848651	3.04536905	Plant height

PH_Meraro	4744	1099369 F 0-26:C>T-26:C>T	5D	548685020	3.2276E-07	0.18258427	178	0.123013483	3.120254331	6.49111775	Plant height
PH_Meraro	6346	1010420 F 0-11:T>G-11:T>G	7B	621404053	0.00059584	0.43258427	178	0.084662238	2.15110397	3.22486876	Plant height
SL_Combined	978	3064524 F 0-21:G>A-21:G>A	2A	117369587	0.00083253	0.154494382	178	0.082111626	0.335928472	3.07960121	Spike length
SL_Combined	1163	1090474 F 0-26:A>G-26:A>G	2A	722320327	0.00065263	0.095505618	178	0.085759896	-0.24820864	3.18533102	Spike length
SL_Combined	4122	3032391 F 0-37:G>T-37:G>T	5B	21636346	0.00046744	0.185393258	178	0.09595973	0.471868254	3.33027616	Spike length
SL_Combined	5186	1863713 F 0-37:C>G-37:C>G	6B	140452409	0.00055266	0.04494382	178	0.087156246	0.280630438	3.25754173	Spike length
SL_Combined	5426	1351797 F 0-16:C>G-16:C>G	6B	708272196	0.00069427	0.053370787	178	0.082235306	0.258443402	3.15847013	Spike length
SL_Combined	5434	3385032 F 0-9:C>T-9:C>T	6B	714009334	0.0009996	0.064606742	178	0.079800016	0.420032879	3.0001734	Spike length
SL_Combined	5442	3956702 F 0-31:C>T-31:C>T	6B	719901771	0.00055979	0.050561798	178	0.086111712	-0.2521334	3.25197446	Spike length
SL_Combined	5629	4910973 F 0-29:C>A-29:C>A	7A	13928165	2.1691E-08	0.047752809	178	0.133494499	0.465614662	7.66371332	Spike length
SL_Holeta	4466	1237690 F 0-23:G>C-23:G>C	5B	604290894	0.00072525	0.112359551	178	0.06633422	0.391337727	3.13951056	Spike length
SL_Holeta	4656	1862935 F 0-26:G>A-26:G>A	5D	490601460	5.4185E-05	0.109550562	178	0.091666438	0.385657278	4.26612451	Spike length
SL_Kulumsa	1330	1023751 F 0-	2B	19448467	0.00065806	0.497191011	178	0.056002789	-0.22616031	3.18173138	Spike length

		40:C>G-40:C>G									
SL_Kulumsa	1331	1104531 F 0-39:T>A-39:T>A	2B	19448572	0.00096589	0.5	178	0.055467965	-0.31475922	3.01507066	Spike length
SL_Kulumsa	2062	2243418 F 0-8:G>C-8:G>C	2D	587648696	0.00018755	0.373595506	178	0.059201374	-0.22660557	3.7268761	Spike length
SL_Kulumsa	3431	1326740 F 0-15:T>G-15:T>G	4A	663673100	0.00062837	0.429775281	178	0.057744008	-0.35252566	3.20178682	Spike length
SL-Meraro	1449	1071933 F 0-52:T>C-52:T>C	2B	105985751	0.00066569	0.056179775	178	0.057785777	-0.28389607	3.17672999	Spike length
SL-Meraro	2602	1026006 F 0-51:A>C-51:A>C	3B	54996488	0.00053953	0.123595506	178	0.059167561	0.203374221	3.26798314	Spike length
SL-Meraro	3805	1263501 F 0-5:A>C-5:A>C	5A	69140651	0.00068344	0.120786517	178	0.057622625	-0.31433873	3.16530243	Spike length
SL-Meraro	4027	3032391 F 0-37:G>T-37:G>T	5A	614408611	3.1745E-11	0.042134831	178	0.077904388	0.240412015	10.4983207	Spike length
SL-Meraro	4441	3955588 F 0-29:T>G-29:T>G	5B	584095441	0.00091449	0.092696629	178	0.056966174	0.294371821	3.03882258	Spike length
SL-Meraro	4508	1694739 F 0-33:A>T-33:A>T	5B	681127665	2.39E-08	0.087078652	178	0.065939653	-0.20349439	7.62161071	Spike length
SL-Meraro	4838	2279397 F 0-55:C>G-55:C>G	6A	29876921	1.563E-10	0.047752809	178	0.068278563	-0.17631552	9.80604037	Spike length
SL-Meraro	4987	1337726 F 0-62:A>G-62:A>G	6A	584694353	0.00094014	0.073033708	178	0.056957017	-0.36848944	3.02680703	Spike length
SL-Meraro	5187	4911245 F 0-46:A>G-46:A>G	6B	140863639	1.6164E-11	0.042134831	178	0.080457965	-0.2269962	10.7914467	Spike length

SL-Meraro	5310	2302989 F 0-59:C>A-59:C>A	6B	598448798	5.3087E-06	0.185393258	178	0.063007773	0.185072716	5.27501265	Spike length
SL-Meraro	6350	2257383 F 0-17:C>G-17:C>G	7B	627604934	4.0367E-05	0.235955056	178	0.061029091	0.188788528	4.39397515	Spike length
SL-Meraro	6563	1089662 F 0-32:G>A-32:G>A	7D	33775394	0.00066021	0.387640449	178	0.059126271	-0.17555162	3.18031811	Spike length
SW_Combined	552	1094239 F 0-18:T>C-18:T>C	1B	593916790	6.6119E-07	0.199438202	178	0.110833189	0.167610095	6.17967428	Spike weight
SW_Combined	745	988503 F 0-5:C>T-5:C>T	1D	72889931	0.0005208	0.18258427	178	0.097951784	0.185610125	3.28333122	Spike weight
SW_Combined	1689	1086456 F 0-25:A>T-25:A>T	2B	683749636	0.00077071	0.148876404	178	0.095010132	0.192920533	3.11310782	Spike weight
SW_Combined	2016	1061891 F 0-7:T>G-7:T>G	2D	508735111	0.00077413	0.075842697	178	0.094095216	0.17113627	3.11118814	Spike weight
SW_Combined	2482	1205701 F 0-28:G>T-28:G>T	3A	733992788	0.00067535	0.140449438	178	0.095461087	0.217306227	3.17047201	Spike weight
SW_Combined	4724	6038202 F 0-6:C>T-6:C>T	5D	541681037	0.00028709	0.058988764	178	0.106651066	0.19296158	3.54198143	Spike weight
SW_Combined	6594	100378184 F 0-25:G>C-25:G>C	7D	65762035	0.00061205	0.098314607	178	0.09548026	0.197494695	3.21321385	Spike weight
SW_Holeta	470	1163534 F 0-6:C>A-6:C>A	1B	529627736	0.00095243	0.148876404	178	0.112601429	-0.12708584	3.02116734	Spike weight
SW_Holeta	508	1667871 F 0-58:G>C-58:G>C	1B	564574913	0.00049022	0.103932584	178	0.12092	-0.18187685	3.30960682	Spike weight
SW_Holeta	1727	1166268 F 0-	2B	717043324	0.00016715	0.404494382	178	0.136449994	0.148825819	3.77689727	Spike weight

		59:T>C-59:T>C									
SW_Holeta	3681	1126513 F 0-64:C>G-64:C>G	4B	662397648	0.00023968	0.241573034	178	0.129333247	-0.14625997	3.62035969	Spike weight
SW_Holeta	4609	996535 F 0-14:G>C-14:G>C	5D	352454245	0.00064447	0.106741573	178	0.119238389	-0.20076336	3.19080024	Spike weight
SW_Holeta	5186	1863713 F 0-37:C>G-37:C>G	6B	140452409	0.00094692	0.04494382	178	0.11288162	-0.14039697	3.02368564	Spike weight
SW_Holeta	5385	1055955 F 0-16:C>T-16:C>T	6B	679360702	0.00089652	0.247191011	178	0.117961393	0.231593691	3.04743776	Spike weight
SW_Holeta	5386	1055955 F 0-58:C>T-58:C>T	6B	679360702	0.00037224	0.221910112	178	0.121302118	-0.14778018	3.42917376	Spike weight
SW_Holeta	5603	1104997 F 0-50:G>T-50:G>T	7A	455502	0.00096583	0.202247191	178	0.112533854	-0.12808558	3.01509809	Spike weight
SW_Holeta	6534	2246599 F 0-51:G>C-51:G>C	7D	14621383	0.00021864	0.47752809	178	0.129418606	0.125132138	3.6602788	Spike weight
SW_Kulumsa	552	1094239 F 0-18:T>C-18:T>C	1B	593916790	0.00049071	0.199438202	178	0.072696629	0.16259984	3.30917702	Spike weight
SW_Kulumsa	554	979184 F 0-40:G>T-40:G>T	1B	594654791	0.00066925	0.143258427	178	0.069957644	0.199889096	3.17441403	Spike weight
SW_Kulumsa	604	5581088 F 0-22:C>G-22:C>G	1B	636134239	0.0005754	0.042134831	178	0.071292623	0.303131704	3.24002854	Spike weight
SW_Kulumsa	630	992991 F 0-9:G>T-9:G>T	1B	647195583	0.00018055	0.370786517	178	0.081524629	-0.15380139	3.74340909	Spike weight
SW_Kulumsa	643	2264416 F 0-15:C>T-15:C>T	1B	660012726	0.0008487	0.146067416	178	0.067865056	0.194641469	3.07124611	Spike weight

SW_Kulumsa	745	988503 F 0-5:C>T-5:C>T	1D	72889931	0.00020809	0.18258427	178	0.08027352	0.189537617	3.6817451	Spike weight
SW_Kulumsa	902	1009798 F 0-9:A>G-9:A>G	2A	30823276	5.5402E-05	0.165730337	178	0.091944642	0.205200842	4.25647727	Spike weight
SW_Kulumsa	986	11309825 F 0-18:C>G-18:C>G	2A	141263053	0.00079925	0.06741573	178	0.068396018	0.277130431	3.0973163	Spike weight
SW_Kulumsa	1318	1074129 F 0-23:T>C-23:T>C	2B	11416837	8.1736E-05	0.081460674	178	0.088520104	0.27711269	4.0875841	Spike weight
SW_Kulumsa	1828	1116814 F 0-17:C>T-17:C>T	2B	770091016	0.00083059	0.230337079	178	0.068053417	0.148561265	3.080612	Spike weight
SW_Kulumsa	1897	978273 F 0-18:G>A-18:G>A	2D	63536670	0.00019821	0.171348315	178	0.080709591	0.181126381	3.70287697	Spike weight
SW_Kulumsa	1898	4911015 F 0-39:T>A-39:T>A	2D	63627645	4.633E-05	0.129213483	178	0.093525774	0.216650573	4.33413618	Spike weight
SW_Kulumsa	2482	1205701 F 0-28:G>T-28:G>T	3A	733992788	0.00012375	0.140449438	178	0.084866056	0.201912328	3.90746159	Spike weight
SW_Kulumsa	2536	1000905 F 0-46:A>G-46:A>G	3B	17785833	0.00037897	0.058988764	178	0.07498197	0.274252631	3.42139575	Spike weight
SW_Kulumsa	4186	1100116 F 0-28:G>A-28:G>A	5B	142427317	0.00024598	0.103932584	178	0.078805368	0.286050315	3.60909545	Spike weight
SW_Meraro	553	5411129 F 0-11:C>T-11:C>T	1B	593916893	0.000298	0.078651685	178	0.095245576	0.468250288	3.52578603	Spike weight
SW_Meraro	1520	1126316 F 0-23:A>G-23:A>G	2B	198011408	1.5962E-08	0.123595506	178	0.110562945	0.545443863	7.79690432	Spike weight
SW_Meraro	2016	1061891 F 0-	2D	508735111	8.2067E-08	0.075842697	178	0.110096619	0.654505131	7.08583341	Spike weight

		7:T>G-7:T>G									
SW_Meraro	2508	7351658 F 0-64:T>C-64:T>C	3B	2491291	2.2352E-10	0.050561798	178	0.117099055	0.604959763	9.65067938	Spike weight
SW_Meraro	2522	3937515 F 0-36:G>T-36:G>T	3B	9775233	0.00099692	0.058988764	178	0.080968767	0.419882123	3.00133845	Spike weight
SW_Meraro	2579	1061107 F 0-49:T>G-49:T>G	3B	29708486	0.0007272	0.31741573	178	0.085819549	0.504925397	3.13834765	Spike weight
SW_Meraro	2582	3022497 F 0-14:T>G-14:T>G	3B	31995400	0.00064146	0.488764045	178	0.086118109	0.458601461	3.1928293	Spike weight
SW_Meraro	2593	1110291 F 0-57:T>G-57:T>G	3B	45271222	0.00090912	0.491573034	178	0.08517302	0.463384725	3.04138047	Spike weight
SW_Meraro	3731	1205054 F 0-57:T>C-57:T>C	4D	465587647	0.00097125	0.202247191	178	0.082508525	0.534924708	3.01266943	Spike weight
SW_Meraro	4629	1094656 F 0-48:G>A-48:G>A	5D	425470918	3.4178E-06	0.064606742	178	0.09899554	0.691471561	5.46625962	Spike weight
SW_Meraro	4724	6038202 F 0-6:C>T-6:C>T	5D	541681037	1.1261E-07	0.058988764	178	0.108029023	0.647865596	6.94842658	Spike weight
SW_Meraro	4849	1234605 F 0-19:A>G-19:A>G	6A	49110792	0.0005065	0.401685393	178	0.090830917	0.504887233	3.29542433	Spike weight
SW_Meraro	4941	4992211 F 0-62:T>C-62:T>C	6A	538546426	4.4744E-06	0.151685393	178	0.09770717	0.55080097	5.34926632	Spike weight
TKW_Combined	626	2263055 F 0-59:G>A-59:G>A	1B	645269217	0.00065696	0.255617978	178	0.133024085	-1.61177468	3.18246322	Thousand kernel weight
TKW_Combined	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.00044308	0.469101124	178	0.138204344	-1.55402373	3.35352004	Thousand kernel weight

TKW_Combined	6402	2264533 F 0-36:C>T-36:C>T	7B	654025136	0.00083538	0.359550562	178	0.12780542	1.55533849	3.07811385	Thousand kernel weight
TKW_Holeta	626	2263055 F 0-59:G>A-59:G>A	1B	645269217	0.00063383	0.255617978	178	0.134435897	-1.71018361	3.19802802	Thousand kernel weight
TKW_Holeta	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.00079039	0.469101124	178	0.128615599	-2.49343174	3.10215625	Thousand kernel weight
TKW_Holeta	6402	2264533 F 0-36:C>T-36:C>T	7B	654025136	0.00051494	0.359550562	178	0.139234309	-1.89599457	3.2882413	Thousand kernel weight
TKW_Kulumsa	626	2263055 F 0-59:G>A-59:G>A	1B	645269217	0.00083181	0.255617978	178	0.130605365	2.511691902	3.07997653	Thousand kernel weight
TKW_Kulumsa	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.00033538	0.469101124	178	0.139328872	-2.47261864	3.47445979	Thousand kernel weight
TKW_Kulumsa	6520	3021078 F 0-6:T>A-6:T>A	7D	6800425	0.00084319	0.373595506	178	0.126200346	-2.42636942	3.07407209	Thousand kernel weight
TKW_Meraro	626	2263055 F 0-59:G>A-59:G>A	1B	645269217	0.0005894	0.255617978	178	0.133084685	-0.51314867	3.22958735	Thousand kernel weight
TKW_Meraro	627	3064575 F 0-60:A>G-60:A>G	1B	646178482	0.0005501	0.469101124	178	0.133326325	-0.47958216	3.25955872	Thousand kernel weight
TKW_Meraro	4921	1714673 F 0-64:C>T-64:C>T	6A	481341158	0.00083183	0.362359551	178	0.126087858	-0.53093117	3.07996432	Thousand kernel weight
TKW_Meraro	6402	2264533 F 0-36:C>T-36:C>T	7B	654025136	0.00059082	0.359550562	178	0.132476524	-0.51937969	3.22854666	Thousand kernel weight

Supplementary table 9. Summary of previously mapped yellow rust resistance QTLs

QTL	Chr	Position (bp)	Previous QTL/gene	Reference
qYRS.01	1A	16417326	Yrsicau-1A, QS.HPAMP_HRU-1A	Fu et al, (2019), Baranwal et al., (2022)
qYRS.02	1A	337947849	<i>QYr.sicau-1AL.1</i>	Yao et al, (2021)
qYRS.03	1A	512496605	<i>QYr.sun 1A_Janz</i>	Zhang et al., (2021)
qYRS.04	1A	588261371	<i>QYr.niab-1A.1</i> , <i>QZn.HPAMP_NarrI-1A</i>	Baranwal et al., (2022)
qYRS.05	1B	50203925	<i>qYr.G</i> , <i>Qyr.wpg_GWAS-1B.2.2</i> ,	Zhang et al., (2021)
qYRS.07	1B	512632641-561151613	QMg.HPAMP_NarrII-2B	Baranwal et al., (2022)
qYRS.08	1B	605007601-687536131	QFe.HPAMP_LDN-2B	Baranwal et al., (2022)
qYRS.09	1D	7734813	<i>QDS.sicau-1D</i> , <i>QYr.hbaas-1DS</i> , <i>QYr-WorldAdult-1DS</i> , <i>Qyr.wpg_GWAS-1D.1</i>	Long et al (2019), Zhang et al., (2021), Baranwal et al., (2022)
qYRS.10	1D	49605264-54911805	MQTL1D.1, QYR.HPAMP_2019LDN-1D	Baranwal et al., (2022)
qYRS.11	1D	244963962	*	-
qYRS.12	2A	733216778-750201766	IZM16, IZM18, Yr1, <i>QYr.inra_2AL.2_CampRemy</i> , <i>QMn.HPAMP_NarrI-2A</i> , <i>QLr-WorldAdult-2AL.2</i> , <i>QYr-WorldAdult-2AL.2</i>	Baranwal et al., (2022), Zhang et al., (2021)
qYRS.13	2B	74203726	Lr23, <i>QRYr2B.2</i> , <i>QYr-WorldAdult-2BS.1</i>	Li, et al (2020), Zhang et al., (2021)
qYRS.14	2B	237588008-243083729	<i>QYrsicau-2B.1</i>	Zhang et al., (2021)
qYRS.15	2B	410189157	<i>QYrww.wgp.2B-3</i>	Mu, et al (2020)
qYRS.16	2B	454344609	*	-
qYRS.17	2B	647897009	*	-
qYRS.18	2B	727221588	*	-
qYRS.19	2B	743311212	<i>QK.HPAMP_HRU-2B.2</i>	Baranwal et al., (2022)
qYRS.20	2B	759523837-768053989	<i>QMn.HPAMP_NarrII-2B</i>	Baranwal et al., (2022)
qYRS.21	2B	790748970-793146869	<i>QYrsicau-2B.1</i> , <i>QS.HPAMP_NarrI-2B</i>	Baranwal et al., (2022)
qYRS.22	2D	74936166	<i>QYr.caas-2DS_Libellulaz</i> , <i>QYr.wpg-2D.1 (IWA1939)</i>	Zhang et al., (2021)
qYRS.23	2D	576290797	<i>QK.HPAMP_NarrII-2D</i>	Baranwal et al., (2022)
qYRS.24	2D	591603469	*	-
qYRS.25	3A	250818410	<i>QSr.ramp-3A.7</i>	Kumar, et al (2020)
qYRS.26	3A	565574116	*	-
qYRS.27	3A	639713075	<i>QYr.rcrrc-3A</i>	Tehseen et al (2022)

qYRS.28	3A	733636208-739951852	QYrCL.sicau-3AL, QLr-WorldAdult-3AL	Yao et al, (2021), Zhang et al., (2021)
qYRS.29	3B	20999249	QYrCL.sicau-3BS.2, QLr-WorldSdlg-3BS, QLR.HPAMP_2018LDN-3B	Chen et al., 2012, Zhang et al., (2021), Baranwal et al., (2022)
qYRS.32	3B	463461507	*	-
qYRS.33	3B	787853986	QYr.ramp-3B.1, Qyr.wpg_GWAS-3B.1	Kumar et al (2020)
qYRS.34	3D	339476105	YR45	Zhang et al., (2021)
qYRS.35	3D	569281482	BS00004334_51	Laura, et al (2022)
qYRS.36	4A	521603853	QYrww.wgp.4A-1	Mu, et al (2020)
qYRS.37	4A	603746204	Yr51, Yr60, IWA3756_APR, QLr-WorldSdlg-4AL	Zhang et al., (2021)
qYRS.38	4B	15149905	Ra_c26080_461, QLr-WorldAdult-4BS.1	Zhang et al., (2021)
qYRS.39	4B	66799362	EPdwGL-4B	Alemu et al, (2020)
qYRS.40	4B	138472187	*	-
qYRS.41	4D	455618789	QYr.hbaas-1DS, QLr.jki-4D.1,QLr.MAGIC_IT-4D.2	Rollar et al., (2021)
qYRS.42	5A	36021495	qYr.J, QYr-WorldAdult-5AS	Zhang et al., (2021)
qYRS.43	5A	429474426	QYr.ramp-5A.1, QLr.MAGIC_IT-5A.1	Kumar et al (2020), Rollar et al., (2021)
qYRS.44	5B	208728682	QYrPI192252.wgp-5BS	Lu et al (2014)
qYRS.45	5D	515407161	*	-
qYRS.46	5D	529525683	*	-
qYRS.47	5D	533205336	QLr-WorldSdlg-5DL	Zhang et al., (2021)
qYRS.48	6A	51769657	BS00011010_51, QDS.sicau-6A., QB.HPAMP_LDN-6A	Long et al (2019), Baranwal et al., (2022)
qYRS.49	6B	8235349	QDS.sicau-6B.1, QYr-WorldAdult-6BS	Zhang et al., (2021)
qYRS.50	6B	291067106	*	-
qYRS.51	6B	476032032-583215607	QFe.HPAMP_LDN-6B	Baranwal et al., (2022)
qYRS.52	6B	664501564	QYr.ucw-6B (IWA7257)	Zhang et al., (2021)
qYRS.53	6B	675702168	QYr.ucw-6B (IWA7257)	Baranwal et al., (2022)
qYRS.54	7A	12800907-50346076	QYr.uga-5B_AGS2000, QLr-WorldAdult-7AS, QYR.HPAMP_2018LDN-7A	Zhang et al., (2021), Baranwal et al., (2022)
qYRS.55	7A	96563306-128909455	EPdwL*- 7A, Qyrsicau-7AS, QLR.HPAMP_2018HRU-7A.1, QK.HPAMP_LDN-7A, QP.HPAMP_LDN-7A	Alemu et al., (2020), Baranwal et al., (2022)
qYRS.56	7A	730639307	QYr.sgi-7A_Kariega	Baranwal et al., (2022)
qYRS.58	7D	353496936	*	-