

**Genetic Analysis for Drought Tolerance and Biomass Allocation in Newly  
Developed Populations of Bread Wheat (*Triticum aestivum* L.)**

**By**

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**A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of  
Philosophy (PhD) in Plant Breeding**

Discipline of Plant Breeding

School of Agricultural, Earth and Environmental Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg

Republic of South Africa

**February 2023**

## Thesis Abstract

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Bread wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ , AABBDD) is the most lucrative commodity crop cultivated worldwide. Wheat productivity is crucial for economic gains and food security to the growing global population. Global wheat production is affected by recurrent droughts that are further exacerbated by a changing climate characterized by rising temperatures and erratic rainfall. In response to these challenges, most wheat breeding programs have focused on increasing harvest index to improve grain yield and drought adaptation without considering below-ground root biomass. In recent years there has been a growing interest in using crops such as wheat to store some of the atmospheric carbon previously lost from soils due to past agricultural practices to sustain soil quality and to mitigate climate change. Increasing biomass allocation of new wheat genotypes to the root system may enhance carbon (C) extraction from the atmosphere and transfer to crop tissues and to soils through carbon sequestration while increasing resilience to drought stress by improving water and nutrient uptake. Therefore, this study aimed at improving drought tolerance and C sequestration ability of wheat for production under dryland farming systems. The specific objectives were:

- i. to provide information based on a retrospective quantitative genetic analysis on combining ability studies of wheat for yield and yield-related traits to predict potential genetic gains achievable in improving biomass allocation for drought tolerance and soil carbon storage;
- ii. to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents;
- iii. to estimate the magnitude of the relationships between root biomass and yield components and to identify influential traits to optimise genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat (*Triticum aestivum* L.);
- iv. to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat to identify good combiners for breeding and enhanced carbon sequestration, and;

- v. to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement.

The first study compared data on the general combining ability (GCA) and specific combining ability (SCA) effects of wheat for yield and related traits under optimum and drought-stressed conditions from 40 studies worldwide. Days to heading (DTH), plant height (PH), number of tillers per plant (TN), kernels per spike (KPS), 1,000-kernel weight (TKW), shoot biomass (SB), and grain yield (GY) exhibited wide variation for GCA and SCA effects. Progeny performance increased by 14.30 and 4.04% for SB and GY, respectively, compared with parental values under optimum water conditions. The number of tillers and SB exhibited positive associations with GY ( $0.45 \leq r \leq 0.85$ ,  $p < 0.05$ ) under both water conditions. Meta effect sizes for drought stress were negative. The highest meta-effect sizes were calculated for DTH (-4.5) followed by SB (-2.0), whereas KPS (-1.25) had the lowest. The genetic gains for PH, SB, and other yield components showed that divergent crosses involving complementary parents could enhance biomass allocation patterns in wheat. This could be used as a basis for improving biomass allocation to roots.

In the second study, a total of 97 bread wheat genotypes were evaluated in field and greenhouse trials under drought-stressed and non-stressed conditions and genotyped using 16 382 high-density single nucleotide polymorphism (SNP) markers. The analysis of molecular variance showed that the intrapopulation variance was very high at 99%, with a small minimal inter-population variance (1%). The genetic distance, polymorphic information content and expected heterozygosity varied from 0.20 to 0.88, 0.24 to 1.00 and 0.29 to 0.58, respectively. The cluster analysis based on SNP data showed that 44% and 28% of the assessed genotypes maintained their genetic groups compared to hierarchical clusters under drought-stressed and non-stressed phenotypic data, respectively. The joint analysis using genotypic and phenotypic data resolved three heterotic groups and allowed the selection of genotypes BW140, BW152, BW157, BW162, LM30, LM47, LM48, LM52, LM54 and LM70. The selected genotypes were the most genetically divergent, with high root biomass and grain yield and are recommended for production or breeding.

The third study evaluated 100 wheat genotypes consisting of 10 parents and 90 derived F<sub>2</sub> families under drought-stressed and non-stressed conditions at two different sites. Data were collected for DTH, days to maturity (DTM), PH, TN, spike length (SL), spikelets per spike (SPS), KPS, TKW,

SB, root biomass (RB), total plant biomass (PB), root-to-shoot ratio (RS) and GY. There was significant ( $p < 0.05$ ) genetic variation in most assessed traits except TN and RS. Root biomass had significant positive correlations with grain yield under drought-stressed ( $r = 0.28$ ) and non-stressed ( $r = 0.41$ ) conditions, but a non-significant correlation was recorded for RS and grain yield. Notably, both root and shoot biomass had significant positive correlations under both water regimes, revealing the potential to increase both traits with minimal biomass trade-offs. The highest positive direct effects on grain yield were found for KPS and PB under both water regimes. The present study demonstrated that selection based on KPS and PB rather than RS will be more effective in ideotype selection of segregating populations for drought tolerance and carbon sequestration potential.

In the fourth study, the above dataset from the ten parental lines and their F<sub>2</sub> progeny were subjected to combining ability analysis using a full-diallel mating design. Significant differences were recorded among the tested families revealing substantial variation for PH, KPS, RB, SB, PB and GY. Additive gene effects conditioned PH, SB, PB and GY under drought, suggesting the polygenic inheritance for drought tolerance. Strong maternal and reciprocal genetic effects were recorded for RB across the testing sites under drought-stressed conditions. The parental line LM75 maintained the GCA effects in a positive and desirable direction for SB, PB and GY. Early generation selection using PH, SB, PB and GY will improve drought tolerance by exploiting additive gene action under drought conditions. Higher RB production may be maintained by a positive selection of male and female parents to capture the significant maternal and reciprocal effects found in this study.

The fifth study showed higher phenotypic coefficient of variation (PCV) than the genotypic coefficient of variation (GCV) for PH, KPS, SB, RB, PB and GY. Moderate heritability of 41.61% and 45.14% and genetic advance as a percentage of the mean (GAM) of 3.49% and 3.58% were observed for RB under drought and for KPS under non-stressed conditions, respectively. Based on correlation and principal component analysis, geometric mean productivity (GMP) and stress tolerance index (STI) were identified as the most efficient drought tolerance indices for selecting drought-tolerant families with high RB. Direct crosses such as BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 were identified as drought

tolerant and are recommended for genetic advancement. The high root biomass production of these families will contribute to carbon inputs through rhizodeposition in agricultural soils. Further research studies should investigate the link between changes in biomass allocation and atmospheric carbon transfer to soils for improving soil quality and mitigating climate change.

The present study revealed that maternal and reciprocal effects should be considered when selecting root biomass and biomass allocation traits. Also, the study identified drought tolerant genotypes and developed new families with high biomass production for enhanced carbon sequestration. The identified families should be advanced for variety development and further evaluated for their net carbon contribution to the soil.

## Declaration

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I, Kwame Wilson Shamuyarira, declare the following.

1. The research reported in this thesis, except where otherwise indicated is my original research.
2. This thesis has not been submitted for any other degree or examination at any other university.
3. This thesis does not contain other persons data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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Signed



Kwame Wilson Shamuyarira

As the candidate's supervisors, we agree to the submission of this thesis:



Prof. Hussein Shimelis (Supervisor)

Dr. Vincent Chaplot (Co-Supervisor)

Dr. Sandiswa Figlan (Co-Supervisor)

## Acknowledgements

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- First of all, I would like to thank Prof. Hussein Shimelis, my supervisor, for his guidance and support throughout this journey. You taught me the need to pay attention to detail and to aim for excellence in my research.
- I would like to thank Dr. Vincent Chaplot for his advice and insights, which were critical in my growth and development as a scientist. You taught me new skills and helped me improve my writing tremendously.
- I am heavily indebted to Dr Sandiswa Figlan and Dr. Rebecca Zengeni for their support and for integrating me into their research teams, in which I broadened my knowledge and understanding of different disciplines in agricultural science.
- This work would not have been possible without the financial support of the National Research Foundation (NRF), African Center for Crop Improvement (ACCI) and Water Research Commission, which is sincerely appreciated.
- Thanks to Dr. Isack Mathew and Dr, Admire Shayanowako for their assistance in data analysis and review of the draft manuscripts.
- I would like to thank the Africa Centre for Crop Improvement (ACCI) technical staff, including Mr Ian Doidge, Susan Vander Merwe and Shadreck Munatsi, for their support in field experiments and management.
- I am grateful to Mrs Rowelda Donnelly and Mrs Lyndre Anderson for their administrative support throughout the entire research period.
- I would like to extend my deepest gratitude to Marylyn Christian and Wanga Maliata Athon, for their assistance during this work.
- Finally, I want to thank my wife, parents and brother for their love, dedication and support through this research. Most importantly, I thank my Lord and Saviour, Jesus Christ, who Has always been a constant guide and protector in my life. May His Name be glorified.

## **Dedication**

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This work is dedicated to my wife, Annahmary, my parents, Lewis and Judith Shamuyarira and my brother, Panashe, for their support throughout the study. May God richly bless you.

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## Abbreviations and Acronyms

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CEF	Controlled Environment Facilities
CIMMYT	International Maize and Wheat Improvement Center
CV	Coefficient of variation
DS	Drought-stressed conditions
DTH	Days to heading
DTM	Days to maturity
F	Inbreeding coefficient
FC	Field capacity
GA	Genetic advance
GCA	General combining ability
GCV	Genotypic coefficient of variation
GY	Grain yield
H <sup>2</sup>	Broad sense heritability
KPS	Kernels per spike
LSD	Least significant difference
MAF	Minor allele frequency
NS	Non-stressed conditions
OP	Optimal conditions
PCA	Principal component analysis
PCV	Phenotypic coefficient of variation
PH	Plant height
PIC	Polymorphic information content
RB	Root biomass
RS	Root to shoot ratio
SB	Shoot biomass
SC	Soil carbon

SCA	Specific combining ability
SEM	Standard error of the mean
SL	Spike length
SNP	Single nucleotide polymorphism
SOC	Soil organic carbon
SPS	Spikelets per spike
SSA	Sub-Saharan Africa
TKW	Thousand kernel weight
TN	Productive tiller number
UKZN	University of KwaZulu-Natal

## Publications Pertaining to This Thesis

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### Chapter 1

Shamuyarira, K.W., H. Shimelis, I. Mathew, R. Zengeni and V. Chaplot. 2022. A meta-analysis of combining ability effects in wheat for agronomic traits and drought adaptation: implications for optimizing biomass allocation. *Crop Science* 62: 139-156. <https://doi.org/10.1002/csc2.20644>

### Chapter 2

Shamuyarira, K.W., H. Shimelis, I. Mathew, A. Shayanowako, R. Zengeni and V. Chaplot. 2022. Comparative genetic diversity analysis for biomass allocation and drought tolerance in wheat. *Agronomy* 12: 1457. <https://doi.org/10.3390/agronomy12061457>

### Chapter 3

Shamuyarira, K.W., H. Shimelis, S. Figlan and V. Chaplot. 2022. Path coefficient and principal component analyses for biomass allocation, drought tolerance and carbon sequestration potential in wheat. *Plants* 11: 1407. <https://doi.org/10.3390/plants11111407>

## Introduction to Thesis

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### Background of study

Bread wheat (*Triticum aestivum* L.,  $2n = 4x = 28$ , AABB) is a staple food for 35- 40% of the global population (Sun et al., 2020). It is highly adaptable and grown worldwide, serving for food security and economic opportunities along the value chains (Li et al., 2018). Currently, the average wheat yield globally is 3.43t/ha, with the highest yields being achieved in Europe and averaging over 4 tons/ha (Sun et al., 2020). In recent years, genetic progress has been slowing, and wheat yield has been leveling worldwide. For instance, yield stagnation in Europe in the last three decades has been caused by increased severity of biotic and abiotic stresses (Le Gouis et al., 2020). In China, yield increases have slowed dramatically since 1997, with only a 1-ton/ha increase observed during this period (Sun et al., 2018). Productivity in Sub-Saharan Africa (SSA) is much lower than in other regions, with yields averaging approximately 2 tons/ha because of increased incidence of climate-related constraints such as drought as well as unfavourable socio-economic conditions that limit investment in breeding and crop management (Tadesse et al., 2019). With wheat consumption rate in SSA rising to 650 million tons per year (Itam et al., 2020), reducing yield losses associated with drought stress can significantly increase yield output and contribute to food security in the region.

Drought negatively affects wheat growth and development by reducing photosynthetic efficiency, water use efficiency, pollen abortion, kernel number and grain yield (Kadam et al., 2014; Sattar et al., 2020). To sustain wheat productivity to meet the demand for a rising world population, irrigation water availability need to be increased by approximately 17% (Itam et al., 2020). Yet it is predicted that by the year 2050, water availability will drop by 50% due to depleting freshwater resources and competing for demand from other industries making irrigation an unsustainable strategy to combat drought stress (Pastor et al., 2020). Under such circumstances, breeding wheat with high water use efficiency and drought tolerance presents the most sustainable way to improve wheat productivity without increasing water demand.

Plants have different strategies that they employ to avoid or tolerate drought. Changes in biomass allocation between shoots and roots are one way through which plants adjust their growth and development to survive under environmental constraints (Liu et al., 2021). Under drought conditions, plants generally alter their root-to-shoot ratio (RS) upwards. High root biomass

fractions have been reported in drier regions than in warmer and humid regions in terrestrial ecosystems (Ma et al., 2021). Zhou et al., (2020) observed a 21% increase in RS under moisture stress in different plant species. Higher RS generally confer drought tolerance in crop plants, and plants with high RS have been associated with higher survival rates and productivity under abiotic stresses (Du et al., 2020). According to Mathew et al. (2019), biomass production and RS ratios vary widely among crop species and crop types. In a study comparing wheat cultivars XC-15 and XC-45 with contrasting stress tolerance levels, Zhang et al., (2020) observed that root dry weight and RS were higher for XC-45, which was more salt tolerant. However, there are reports arguing that an increase in root-to-shoot ratio can compromise the yield potential of crops in favour of plant survival under stress which would negate the purpose of drought tolerance breeding (Passioura 1983; Liu et al., 2004; Bakhshandeh et al., 2019). Therefore, plant breeders should be careful to manage possible biomass trade-offs between roots and shoots that may compromise yield potential in wheat (Thorup-Kristensen et al., 2020).

The allocation of biomass between roots and shoots is an important link between atmospheric and soil carbon (Zhou et al., 2020). Conversion of atmospheric carbon through photosynthesis can be manipulated through plant breeding to increase biomass partitioning to the roots for climate change mitigation (Panchal et al., 2022). Crops with higher root biomass contribute more soil carbon inputs via rhizodeposition and dead root tissue, while concurrently improving wheat's resilience and yield potential in drier climates (Kell 2011). Higher carbon sequestration levels have been reported in drier than in wet environments (Zhou et al., 2022). According to Fan et al. (2019), crops (e.g. canola, legumes, maize and wheat) with high root biomass increased carbon inputs by 81% in 44 years and changed Canadian agricultural lands from a carbon source into a carbon sink. Breeding for the dual purpose of drought tolerance and carbon sequestration symbolizes a climate-smart approach to reduce the impact of climate on agriculture with minimal demands for crop management practices.

To initiate the breeding process, breeders should evaluate the level of genetic diversity available for targeted traits in the available germplasm (Li et al., 2018). Collection and characterization of germplasm with a broad genetic base is a prerequisite for the successful implementation of any breeding program that will achieve genetic gains (Abou-Elwafa and Shahzad 2021). The International Maize and Wheat Improvement Center (CIMMYT) has the largest wheat germplasm

collection globally from which breeders can source genetic resources for breeding wheat for diverse agronomic zones (Sobhaninan et al., 2019). Phenotypic characterization of crop plants was the major way to categorize and differentiate genotypes for breeding purposes. But the advent of DNA markers has further facilitated the classification of genotypes using both morphological and molecular markers to elucidate the level of genetic diversity in germplasm collections (Agre et al., 2019). Amongst the DNA markers, single nucleotide polymorphism (SNP) markers have gained prominence in genetic diversity analysis due to wide distribution across the genome, genetic stability, compatibility with automation and ease of genotyping (Mammadov et al., 2012; Chung et al., 2017). Characterizing different accessions and genetic stocks from CIMMYT using phenotypic traits and SNP markers would assist in selecting genetically diverse material that can be used to generate new breeding populations.

Improving wheat for biomass allocation, yield and drought tolerance requires understanding the inter-relationships among morphological traits under drought-stressed and non-stressed growing conditions (Toyinbo et al., 2021). Information on correlations between traits allows breeders to focus on traits with the strongest relationships with grain yield and discard trait evaluations with minimum impact (Patil et al., 2018). According to Mphahlele et al. (2021), positively correlated traits share genetic regions or linkage between genes and can be selected together to increase selection efficiency. On the other hand, negative relationships between quantitative traits can complicate the direction of selection which may stall genetic progress (Neyhart et al., 2029). This may require a change in breeding strategy and necessitate the prior selection of quantitatively inherited traits at early generations and further selection or introgression of simply inherited traits in advanced generations.

The performance of selected genotypes is not an indicator of their ability to pass on favourable alleles and produce superior progeny. Therefore, it is imperative for breeders to assess the value of selected lines by combining ability analysis for backward selection of parents that can be used in well-designed crosses and forward selection of progeny for genetic advancement. General combining ability (GCA) of parents refers to the average contribution of the parent to its progeny while the specific combining ability (SCA) refer to the deviation of hybrids from the expected contribution of the parent. High GCA effects are of great importance for line breeding as they allow for selecting polygenic traits at succeeding generations and capturing a large proportion of

the variation. High GCA than SCA effects reflect a predominance of additive gene action over dominance and epistasis (Zhou et al., 2018). Knowledge of the predominant gene action controlling important traits will determine whether a breeder would employ hybrid breeding or pursue pure-line and pedigree breeding (Younas et al., 2020) to improve biomass allocation and drought tolerance. In pure line breeding, populations should be evaluated for combining ability at early generations to reduce the cost of assessing large populations at advanced generations (Yu et al., 2020).

Most combining ability analysis of crops overlooks the contribution of maternal inheritance based on the assumption that they are not present (Chaudhary et al., 2022; Thungo et al., 2022). However, the inheritance of biomass allocation, yield and drought tolerance may be influenced by cytoplasmic DNA or may include an interaction of nuclear and cytoplasmic factors (Satyavathi et al., 2016). Inheritance of cytoplasmic DNA from female parents is responsible for the phenotypic differences that are observed in reciprocal crosses (Gimenez et al., 2021). Therefore, genetic analysis that does not provide information on maternal and reciprocal effects may underestimate the value of lines in making superior crosses when they are used as female parents (Yao et al., 2013). To improve the selection efficiency of plant breeding programs, reciprocal crosses should be included in the genetic analysis. This will help identify the most efficient direction of crosses that will promote the introgression of desirable maternal genes into progeny (Ofori and Padi 2020).

Understanding the genetic variability in segregating populations and determining quantitative genetic information to inform the plant breeding strategy is essential. Progress in breeding under different levels of moisture availability depends on an in-depth understanding of trait heritability and estimates of genetic advance (Sobhaninan et al., 2019). Heritability estimates indicate the selection accuracy based on a crop phenotype and the response to selection that can be expected depending on the selection pressure applied (Tokatlidis et al., 2010). Therefore, selection effectiveness for quantitative traits such as biomass allocation and drought tolerance increase when heritability is high. This will ensure higher genetic gains through early generation selection (Agaba et al., 2021). However, heritability and genetic advance estimates are often low under water-limited conditions, thus impeding genetic progress (Farid et al., 2017). Furthermore, selection for drought tolerance is confounded by the environment, with genotypes changing rankings depending on stress severity, plant genetics and genotype by environment interaction. Therefore, it is essential

to use an efficient selection index that will identify drought-tolerant genotypes that meet farmers' yield expectations and have optimized biomass allocation for enhanced carbon sequestration for climate change mitigation.

### **Rationale of study**

Climate change induced drought is the major abiotic stress that affects dryland wheat production in South Africa and other wheat-growing regions of SSA. This has led to reduced profitability for wheat farmers and a declined cultivation area as farmers switch to alternative crops to remain profitable. Developing cultivars that are high yielding and stable under fluctuating moisture availability will increase the resilience of wheat production in rain-fed regions of SSA and encourage farmers to maintain or expand wheat cultivation area.

Drought tolerance screening is complex and requires rigorous evaluation of crops under different moisture conditions. The capacity of plants to withstand drought depends on their water use efficiency and ability to extract water deep in the soil profile when water is scarce. Therefore, developing wheat cultivars with increased biomass allocation to the root system will improve water and nutrient uptake at critical growth stages to support yield formation. In addition, wheat with higher root biomass will deposit more carbon in the soil, which will be critical for carbon extraction from the atmosphere and sequestration to the soil for climate change mitigation. No current breeding program in South Africa is focused on development of varieties to increase carbon sequestration for climate change mitigation. In addition, these varieties may provide farmers with a potential second source of income from obtaining carbon credits by planting these varieties. Therefore, there is need to identify elite parents that will be used to develop new breeding populations from which to select transgressive segregates with high drought tolerance and root biomass production. The selected genotypes should be advanced for variety development and deployment to farmers.

### **Overall research objective**

To improve drought tolerance and C sequestration ability in wheat genotypes for production under dryland farming systems

### **Specific objectives**

- i. to provide information based on a retrospective quantitative genetic analysis on combining ability studies of wheat for yield and yield-related traits to predict potential genetic gains achievable in improving biomass allocation for drought tolerance and soil carbon storage;
- ii. to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents;
- iii. to estimate the magnitude of the relationships between root biomass and yield components and to identify influential traits to optimise genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat (*Triticum aestivum* L.);
- iv. to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat to identify good combiners for breeding and enhanced carbon sequestration, and;
- v. to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement.

### **Hypotheses**

- i. Genetic gains are achievable for biomass allocation, drought tolerance and soil carbon storage in wheat
- ii. There is sufficient genetic variation in wheat germplasm collections for biomass allocation and drought tolerance
- iii. There are relationships between root biomass and yield components that can influence genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat
- iv. Maternal effects are influential in controlling yield-related traits and biomass allocation in wheat
- v. Genetic variability is present in the developed wheat populations for grain yield and biomass allocation under different water stress conditions

## Outline of thesis

The thesis consists of five chapters in accordance with the number of objectives (Table 0.1). The thesis is written in the form of different research chapters, each following the format of a stand-alone research paper followed by a general overview and implications of findings from the study. This is the dominant thesis format adopted by the University of KwaZulu-Natal. Consequently, there are some overlaps and unavoidable repetitions of references and some introductory information between chapters. The referencing style used in this thesis is based on the Journal of Crop Science referencing system.

Table 0.1 Outline of thesis

Chapter	Title
-	Introduction to Thesis
1	Literature Review: A Meta-analysis of Combining Ability Effects in Wheat for Agronomic Traits and Drought Adaptation: Implications for Optimizing Biomass Allocation
2	Comparative Genetic Diversity Analysis for Biomass Allocation and Drought Tolerance in Wheat
3	Path Coefficient and Principal Component Analyses for Biomass Allocation, Drought Tolerance and Carbon Sequestration Potential in Wheat
4	Genetic Analysis of Yield and Yield-related Traits and Biomass Allocation in Newly Developed Wheat Populations
5	Advancing Grain Yield, Drought Adaption and Biomass Allocation in Wheat Populations
-	General Overview and Implications for Breeding

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# Chapter 1: Literature Review: A Meta-analysis of Combining Ability Effects in Wheat for Agronomic Traits and Drought Adaptation: Implications for Optimizing Biomass Allocation

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## Abstract

Combining ability effects for yield-related traits can serve as selection criteria to pursue breeding for optimal biomass allocation in wheat (*Triticum aestivum* L.). The objective of this paper is to provide information based on a retrospective quantitative genetic analysis on combining ability studies of wheat for yield and yield-related traits to predict potential genetic gains achievable in improving biomass allocation for drought tolerance and soil carbon storage. The study compared data on the general combining ability (GCA) and specific combining ability (SCA) effects of wheat for yield and related traits under optimum and drought-stressed conditions from 40 studies worldwide. Days to heading (DTH), plant height (PH), number of tillers per plant (TN), kernels per spike (KPS), 1,000-kernel weight (TKW), shoot biomass (SB), and grain yield (GY) exhibited wide variation for GCA and SCA effects. Progeny performance increased by 14.30 and 4.04% for SB and GY, respectively, compared with parental values under optimum water conditions. The number of tillers and SB exhibited positive associations with GY ( $0.45 \leq r \leq 0.85$ ,  $p < 0.05$ ) under both water conditions. Meta effect sizes for drought stress were negative. The highest meta-effect sizes were calculated for DTH (-4.5) followed by SB (-2.0), whereas KPS (-1.25) had the lowest. The genetic gains for PH, SB, and other yield components showed that divergent crosses involving complementary parents could enhance biomass allocation patterns in wheat. This could be used as a basis for improving biomass allocation to roots.

**Keywords:** *Combining ability effects, Drought tolerance, Meta-analysis, Soil carbon, Wheat*

## 1.1 Introduction

Adverse weather conditions such as unpredictable rainfall patterns and excessive temperatures due to climate change have a negative impact on crop production (Beacham et al., 2018). According to Zhang et al., (2018), climate change induced drought stress is the major limiting factor of crop production around the world. However, the impact of drought stress varies with genotypic differences (Rampino et al., 2006). Assessing genetic variation and identifying heritable traits that confer yield advantage under water limited conditions is important for developing suitable varieties. Plants are known to alter their biomass partitioning in response to drought stress and biomass allocation has been identified as a drought adaptive trait. Therefore, improving biomass allocation pattern in crops provides an opportunity to improve drought tolerance.

Grain yield is the primary trait for most breeding programs such that modern wheat (*Triticum aestivum* L.) cultivars are optimized for high harvest indices (Kobata et al., 2018) However, modern wheat cultivars are highly susceptible to drought stress due to the high harvest indices and compromised root systems that are less efficient in water and nutrient acquisition compared to obsolete varieties and landraces (White et al., 2015). Altering biomass allocation pattern in wheat to increase root biomass would potentially improve tolerance to drought stress and nutrient deficiencies (Yu et al., 2016), especially in agricultural systems where wheat experiences terminal drought stress and depends on moisture stored in deeper soil horizons. However, breeding for increased root biomass is complicated by the difficulty of root sampling and high environmental error observed in phenotyping root traits (Lynch, 2007), and possible source–sink competition for photosynthates with yield vessels (Shokat et al., 2020). Proxy traits have been used successfully for indirect selection to improve grain yield (GY) under favourable moisture conditions. Assessing genetic gains using proxy traits can provide vital information to predict genetic gains under drought conditions. Similarly, genetic gains in above ground traits and their relationship with GY can be used to predict possible improvement in rooting ability and its impact on GY.

The number of kernels per spike (KPS), 1,000-kernel weight (TKW), and the number of spikes per unit area (NS) are the most important yield components used for indirect selection for GY in wheat (Simmonds, et al., 2014). The success in improving the yield potential of current elite cultivars has been the result of increases in KPS (Basile, et al., 2019). In a study involving 26 bread wheat genotypes grown at different periods between 1940 and 2000, Sanchez-Garcia, et al. (2013)

observed that yield improvement was a result of a 0.3% and 0.6% increase per year of NS and KPS, respectively. These observations indicate that much of yield improvement in wheat has resulted from improving aboveground traits related to GY. The high number of KPS and kernel weight are highly sensitive to environmental fluctuations, which predisposes wheat to abiotic stresses such as heat and drought. Furthermore, increase in wheat productivity is likely to be realized from optimized biomass allocation because most of the yield related traits have reached their maximum genetic potential (Sadras and Lawson, 2011; Sanchez-Garcia, et al., 2013).

Biomass allocation in modern cultivars is not optimized for stress tolerance but high yield under favourable conditions. The objective of this paper is to compare parent and progeny performance for yield and yield-related traits and drought adaptation in wheat based on a retrospective meta-analysis of combining ability studies to predict genetic gains and guide selection with optimal biomass allocation. The premise of this study is that targeting biomass allocation for cultivar selection provides an opportunity for breeding to improve wheat resilience under sub-optimum environments.

## **1.2 Materials and methods**

### **1.2.1 Study set-up**

Data were collected from studies on combining ability effects of wheat for agronomic traits under drought-stressed and optimum moisture conditions which were published in peer reviewed journals. The literature was searched from electronic databases including Google Scholar, Web of Science, and Scopus using the following keywords: wheat, biomass allocation, root biomass, shoot biomass, combining ability effect, general combining ability, specific combining ability, GCA, SCA, genetic analysis, additive gene action, and non-additive gene action. The data were limited to wheat only while there was no delimitation on period of the studies or whether they were conducted under greenhouse or field conditions. For a study to be selected, it had to provide data on the mean performance, general combining ability (GCA) of parents and specific combining ability (SCA) effects of crosses for yield and yield related traits. The yield related traits included days to heading (DTH) and days to maturity (DTM), plant height (PH), number of tillers per plant (TN), spike length (SL), spikelets per spike (SPS), KPS, TKW, shoot biomass (SB), and GY. These traits are directly related to biomass allocation as they influence plant phenology and biomass accumulation capability. In some instances, these variables were deduced from related information

provided in the studies. After selecting studies that met the selection criteria, data was extracted and compiled into a database. The database captured information including names of authors, year of publication, location of experimental sites, design of the experiment, treatment, plant population, and the generation of genotypes used in the studies. Experiments detailing 1,440 observations in 40 peer reviewed journal articles (Appendix 1.1) were obtained using the selection criteria mentioned above. Links to the studies used in this meta-analysis are listed in Appendix 1.2.

### **1.2.2 Definition of environmental and genetic variables**

The studies consisted of observations carried out under different soil moisture availability and were duly divided between drought stressed and optimum treatments. The observations that were grouped under the optimum treatment were considered to be observations made on a crop that received adequate moisture without any significant moisture stress as reported in the respective studies. In contrast, the observations grouped under drought stress treatment were made on crops grown with limited moisture availability that induced significant drought stress compared to the control treatment as reported by the respective studies. Studies that did not provide a comparison in terms of water availability were assumed to have been conducted under optimum water availability (Saeed et al., 2016; Yao et al., 2011). Finally, there were studies that reported multiple levels of water availability, and in such cases only the maximum and minimum levels were regarded as optimum and drought stressed conditions, respectively.

The generation of the wheat families constitute genetic factors that influence agronomic performance. Generations were separated between parents and progenies to reduce the confounding effects of the genetic background. Parents were the genotypes used in generating progenies through crosses whereas the progenies were either the first filial generation ( $F_1$ ) or the second filial generation ( $F_2$ ).

### **1.2.3 Definition of agronomic variables**

Yield and yield related traits used in this analysis were defined for the purpose of this analysis (Table 1.1). A total of seven selected agronomic variables influencing wheat production and productivity were captured in the databases. The number of DTH were defined as the number of days taken for 50% of the plant population in a plot to have emerged spikes, and the number of DTM was the time taken for 50% of plants to reach physiological maturity as described in most

studies. Number of tillers per plant was expressed as the TN counted on an individual plant based on sampled number of plants per genotype. Where the tillers were recorded per plot, the number was averaged across the number of plants in the particular plot to normalize the data. Plant height was the average height from the soil surface to the tip of the spike, and where the studies indicated that spikes were excluded from the PH, the average length of the spike was added to make up the shortfall in PH. Kernels per spike was measured as the number of kernels that were harvested from individual spikes. Thousand kernel weight was the total weight of 1,000 sampled kernels in g from each genotype and where kernel weight was recorded differently, it was standardized to the weight of 1,000 kernels. Shoot biomass was the total weight of aboveground biomass including leaves and stems but excluding the grain. The SB was standardized to  $\text{g m}^{-2}$  using the available plant population density. The GY was extracted from the papers and normalized to  $\text{g m}^{-2}$  using the provided plot space and population density. The average planting density of 50 plants  $\text{m}^{-2}$  was used in cases where the population density was not provided, and the GY was adjusted accordingly.

Table 1.1. Definition of agronomic and yield related traits used in this study

<b>Variable</b>	<b>Symbol</b>	<b>Units</b>	<b>Definition</b>
Days to heading	DTH		the number of days from sowing until 50% of the plants had fully emerged spikes
Plant height	PH	cm	the height from base of the plant at the soil surface to the base of the spike
Number of tillers per plant	TN		the number of tillers that had managed to set seed
Kernels per spike	KPS		the number of kernels per individual spike
Thousand kernel weight	TKW	g	the total weight of 1000 individual grains
Shoot biomass	SB	$\text{g/m}^2$	the total weight of above ground biomass (leaves and stems) excluding grain
Grain yield	GY	$\text{g/m}^2$	the total weight of harvestable grains

#### 1.2.4 Data analyses

The data collected were tested for normality, outliers, linearity, and homoscedasticity prior to statistical analyses. The data was normalized by the plant population and plot space. The distribution and variability of the means, GCA, and SCA effects were summarized using boxplots. The box plots showed the distribution of the data using the minimum, maximum, mean and the first and third quartile values within the fifth and 95th percentiles after removal of outliers. Pearson correlation and principal component analyses were carried out using R software (R Core Team,

2019) to determine the bivariate and multivariate associations, respectively. The principal component analysis (PCA) was uncentred to convert nonlinear factors and variables into linear combinations. The effects of drought stress on biomass and yield production and water use efficiency were calculated by comparing the datasets and deducing the mean effect size using MetaEasy software v1.0.2 (Kontopantelis and Reeves, 2009). The MetaEasy software assists in standardizing the effect size and increases statistical precision and reduces bias in data by factoring in sample sizes (Kontopantelis and Reeves, 2009). The Cochrane Collaboration (Stokes et al., 2015) was used in the meta-analysis of the data. The effect sizes were estimated within 95% confidence interval based on the Dersimonian–Laird (DL) random effects model that accounts for heterogeneous studies (DerSimonian and Laird, 1986). An effect size whose cumulative value did not cross the zero line of the biplot was considered significant.

## **1.3 Results**

### **1.3.1 Variation of mean values, GCA, and SCA effects of agronomic traits**

There was wide variation in trait performance among the wheat genotypes evaluated across the studies (Table 1.2). The coefficients of variation ranged between 3.45% and 56.63% suggesting that trait mean performance varied considerably among the different genotypes across the studies. Days to heading varied from 75 to 132. Days to heading and PH exhibited the lowest variation with a coefficient of variation value of 3.45% and 11.5%, respectively, under drought conditions. The tallest plants were 120 cm and the shortest were 67 cm. Tillering capacity varied widely with maximum attainable tillers being 25 tillers per plant, whereas the least tillering genotypes had 2 tillers per plant. The number of KPS varied between 27 and 69, whereas TKW ranged from 28.50 to 58.67 g. Shoot biomass and GY exhibited coefficients of variation values of 42.80% and 56.52%, respectively. The SB had a range between 538.00 and 3,838.00 g m<sup>-2</sup>. The maximum attainable GY was 1,448.00 g m<sup>-2</sup> and a minimum of 159.20 g m<sup>-2</sup> was observed. The skewness and kurtosis values for all the traits were between -1 and 1 indicating that the data could be described as normally distributed.

Table 1.2. Summary statistics of agronomic and yield related traits

Statistics	DTH		PH		TN		KPS		TKW		SB		GY	
	OP	DS	OP	DS	OP	DS	OP	DS	OP	DS	OP	DS	OP	DS
<b>N</b>	262	14	548	130	446	134	513	181	665	144	183	33	801	153
<b>Mean</b>	96.59	89.06	92.08	99.54	8.76	3.18	51.16	43.49	45.09	43.83	2385.00	788.30	601.80	327.10
<b>Median</b>	95.00	88.50	92.19	101.10	8.67	3.11	52.25	43.94	45.91	42.62	2093.00	777.00	509.30	233.60
<b>Min.</b>	75.33	84.30	67.00	83.95	3.63	2.43	26.50	26.88	28.50	33.81	813.30	538.00	217.60	159.20
<b>Max.</b>	132.30	96.00	112.40	120.40	25.33	4.30	68.93	68.46	58.67	57.13	3838.00	1179.00	1448.00	890.00
<b>Range</b>	56.97	11.70	45.41	36.49	21.70	1.87	42.43	41.58	30.17	23.32	3025.00	641.00	1230.00	730.80
<b>Q1</b>	84.30	87.00	83.53	91.80	5.50	2.80	45.10	38.98	39.46	38.72	1837.00	692.50	340.20	208.50
<b>Q3</b>	105.00	91.00	101.00	106.80	10.73	3.50	59.00	47.96	50.71	47.38	3115.00	852.20	817.10	388.00
<b>SD</b>	15.62	3.07	10.68	8.78	3.68	0.46	10.09	7.42	7.34	6.31	763.00	135.90	315.80	185.20
<b>SEM</b>	0.97	0.82	0.46	0.77	0.17	0.04	0.45	0.55	0.29	0.53	56.40	23.66	11.16	14.98
<b>CV (%)</b>	16.18	3.45	11.60	8.82	42.03	14.31	19.72	17.07	16.28	14.40	32.00	17.24	52.48	56.63
<b>Skewness</b>	0.54	0.56	-0.12	-0.12	0.89	0.26	-0.50	-0.04	-0.20	0.52	0.37	0.70	0.83	1.40
<b>Kurtosis</b>	-0.65	0.03	-0.96	-1.23	1.47	-0.86	-0.50	0.03	-0.84	-0.81	-1.04	0.63	-0.30	0.58

N = number of observations, Min. = minimum, Max = maximum, Q1 = first quartile, Q3 = third quartile, SD = standard deviation, SEM = standard error of mean, CV = coefficient of variation, DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB (g/m<sup>2</sup>) = shoot biomass and GY (g/m<sup>2</sup>) = grain yield, OP = optimal conditions, DS = drought stressed conditions

Under optimal conditions, the progeny flowered in 96 days which was 4.07% earlier than the parents that flowered in 102 days (Appendix 1.3). The progenies and parents exhibited no significant variation in heading time under drought conditions although they both flowered earlier than under optimal conditions (Appendix 1.3). The GCA effects for DTH were similar between drought and optimal conditions (Appendix 1.4), whereas Appendix 1.4 shows that SCA effects for DTH were significantly higher under optimal compared to drought conditions.

The average height for the progenies was 104.87 cm which was 3.10% taller than the parents under optimal conditions (Appendix 1.3). The average height of progeny was similar to that of the parents at about 100 cm under drought conditions (Appendix 1.3). The GCA effects for PH were similar under drought and optimal conditions (Appendix 1.4), whereas there was a slight decrease in SCA effects for PH under drought conditions (Appendix 1.4). The tillering capacity of the progeny was lower than that of the parents under optimal conditions with respective means of 9 and 12 tillers per plant (Figure 1.1). Under drought conditions, the tillering capacities of both parents and progeny were reduced significantly by over 70%, although the average TN for parents and progeny were similar under drought conditions (Figure 1.1). The average GCA and SCA effects for TN were similar under both drought and optimum conditions although SCA effects exhibited wider variation under drought conditions.

The parental and progeny means for KPS were the same under optimal conditions (Appendix 1.5). In comparison, the mean KPS values for parents and progeny were 12.35% and 13.07% lower, respectively, under drought conditions (Appendix 1.5). Wider variation for the GCA effects for KPS were observed under drought than under optimal conditions (Appendix 1.6), whereas the means and variation for the SCA effects for KPS were higher under optimal conditions than under drought conditions (Appendix 1.6). The mean TKW of the progeny was 4.91% and 14.16% higher than that of the parents under optimum and drought conditions, respectively (Appendix 1.5). There was wider variation for the GCA effects and SCA effects for TKW under drought conditions compared to optimal conditions (Appendix 1.6). The progeny exhibited a higher capacity to accumulate SB than the parents under control conditions. The average SB for progeny was 2419.41 g m<sup>-2</sup> compared to 2336.03 g m<sup>-2</sup> for parents under optimum conditions (Figure 1.1). The average values for SB for parents and progeny were reduced by 65.44% and 67.22%, respectively, under

drought conditions (Figure 1.1). The GCA and SCA effects for SB exhibited wider variation under optimum conditions compared to drought conditions (Figure 1.2). The progeny attained higher mean GY of  $750.88 \text{ g m}^{-2}$  compared to  $658.68 \text{ g m}^{-2}$  recorded for the parents under optimal conditions (Figure 1.1). Similarly, the mean values for GY for progeny and parents were  $433.68$  and  $405.88 \text{ g m}^{-2}$  under drought stress conditions which corresponded to 42.24% and 38.38% reduction in GY, respectively, compared to optimal conditions (Figure 1.1). The GCA effects for GY exhibited wider variation and were slightly higher under optimal conditions than drought stress conditions, whereas the SCA effects for GY were higher and more variable under optimum conditions than under drought conditions (Figure 1.2).

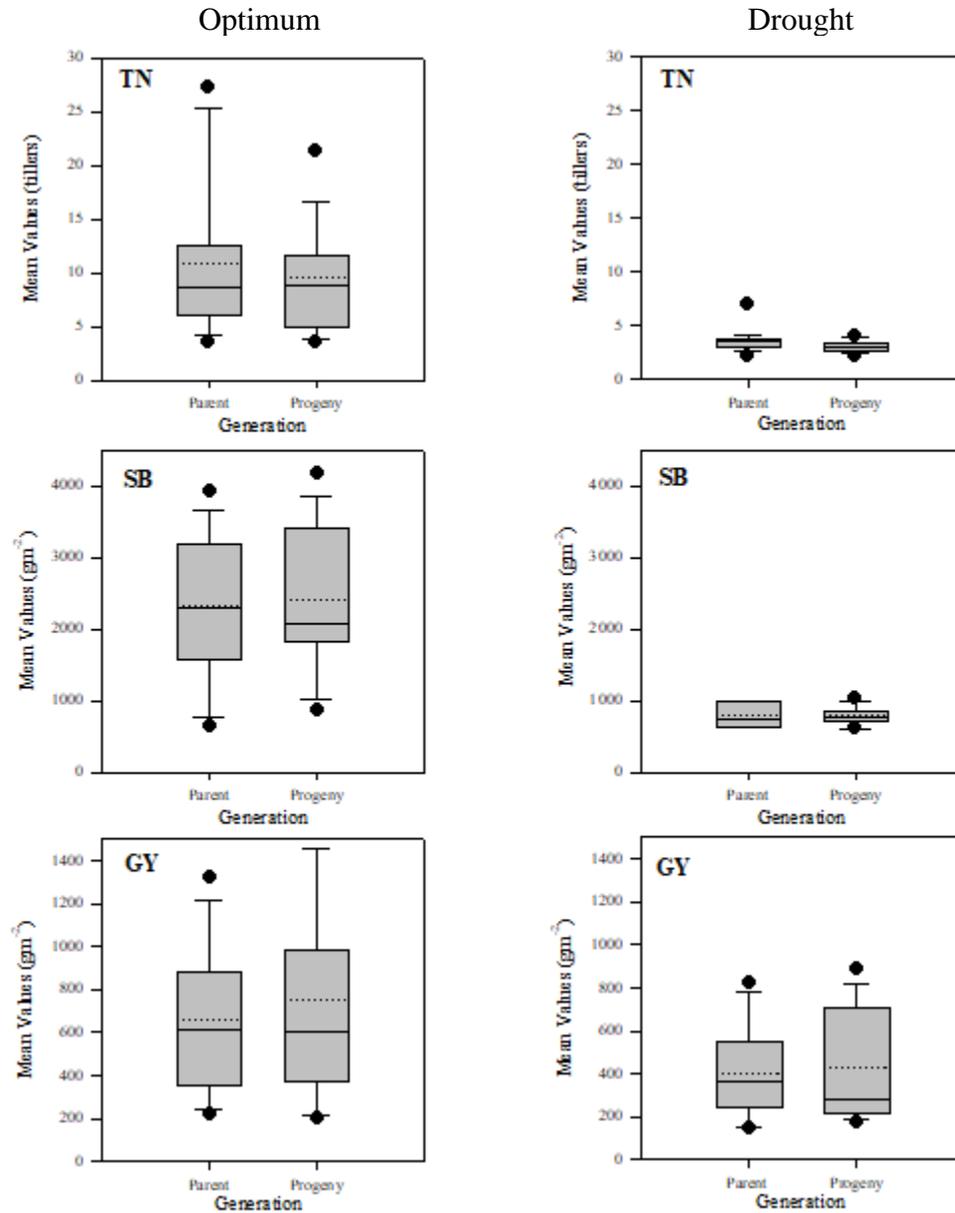


Figure 1.1. Box plots showing the distribution of mean values for number of tillers per plant (TN), shoot biomass (SB) and grain yield (GY) under optimum (left side) and drought (right side) conditions

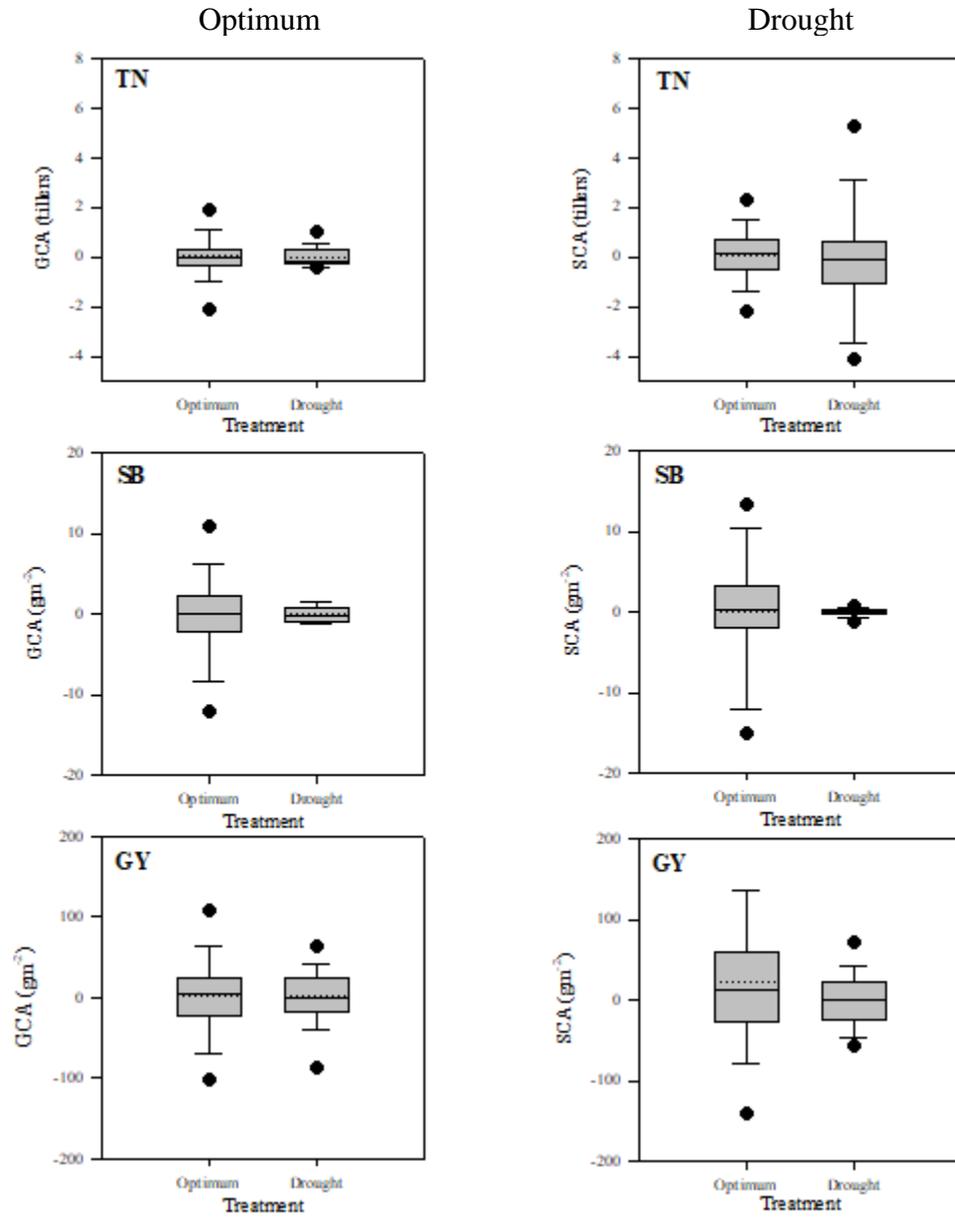


Figure 1.2. Box plots showing the distribution of general combining ability (GCA) and specific combining ability (SCA) for number of tillers per plant (TN), shoot biomass (SB) and grain yield (GY) under optimum and drought conditions

### 1.3.2 Association among yield related traits

#### 1.1.1.1 Correlation analysis

The Pearson correlation coefficients (Table 1.3) showed that GY exhibited significant ( $p < 0.05$ ) and positive correlations with TN ( $r = 0.71$ ) and SB ( $r = 0.45$ ) and exhibited a negative correlation with DTH ( $r = -0.60$ ,  $p < 0.05$ ). Under drought conditions, GY was significantly ( $p < 0.05$ ) and positively correlated to PH ( $r = 0.27$ ), TN ( $r = 0.54$ ), KPS ( $r = 0.20$ ), and SB ( $r = 0.85$ ). On the other hand, there were variable associations among the yield related traits under both optimal and drought conditions. For instance, SB exhibited positive and significant correlations with all the other traits under optimal conditions yet was only correlated with GY under drought conditions. The strongest correlation under optimal conditions was recorded between SB and PH ( $r = 0.94$ ,  $p < 0.05$ ). Under drought conditions, TKW was negatively associated with PH, TN, and KPS whereas TN and KPS were positively correlated to PH.

Table 1.3. Pearson correlation coefficients under drought (above diagonal) and optimum (below diagonal) conditions calculated from agronomic trait values reported in different studies

Traits	DTH	PH	TN	KPS	TKW	SB	GY	
<b>DTH</b>	1	0	0.02	0.05	0.16	-0.05	0.24	
<b>PH</b>	-0.44*	1	0.13*	0.71*	-0.50*	-0.05	0.27*	
<b>TN</b>	0.47*	-0.32*	1	0.08	-0.19*	0.11	0.54*	
<b>KPS</b>	-0.69*	0.04	-0.04	1	-0.52*	0.04	0.20*	<b>Drought</b>
<b>TKW</b>	-0.85*	0.02	-0.05	0	1	0.01	-0.11	
<b>SB</b>	0.57*	0.94*	0.58*	0.53*	-0.85*	1	0.85*	
<b>GY</b>	-0.60*	0.01	0.71*	-0.02	-0.05	0.45*	1	
<b>Optimum</b>								

\* Significant at  $P \leq 0.05$ , DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB ( $g/m^2$ ) = shoot biomass and GY ( $g/m^2$ ) = grain yield

#### 1.1.1.2 Principal component analysis

The rotated principal component (PC) matrix (Table 1.4) showed that the relative contributions of the different traits to the principal components varied significantly under the different water regimes. About 53.64% of the total variation under optimal conditions was explained by the first three PCs with eigenvalues greater than one. The highest contributing traits on the first PC were SB and PH, which contributed above 0.30 each. The variation on the second PC was dominated by TN and GY, whereas the variation on the third PC was largely contributed by DTH. Under

drought conditions, 59.7% of the variation was attributable to the first three PCs. The dominant traits on the first PC were PH and KPS, with above 0.30 contribution each. Grain yield and SB contributed to loading scores of 0.45 and 0.31, respectively, accounting to the variation explained by the second PC. On the third PC, DTH (0.58) and TN (0.31) were the major contributors to the explained variation of 14.67%.

Table 1.4. Rotated component matrix of agronomic and yield related traits under control and drought conditions

Parameters	Optimum			Drought		
	PC1	PC2	PC3	PC1	PC2	PC3
<b>Eigenvalue</b>	1.37	1.25	1.14	2.07	1.08	1.03
<b>Variance percent (%)</b>	19.53	17.79	16.33	29.63	15.45	14.67
<b>Cumulative variance (%)</b>	19.53	37.32	53.64	29.63	45.08	59.75
<b>DTH</b>	0.08	0.00	0.62	0.00	0.09	0.58
<b>PH</b>	0.31	0.21	0.00	0.34	0.03	0.03
<b>TN</b>	0.00	0.45	0.06	0.03	0.12	0.31
<b>KPS</b>	0.00	0.03	0.00	0.31	0.00	0.05
<b>TKW</b>	0.00	0.05	0.05	0.30	0.01	0.03
<b>SB</b>	0.36	0.01	0.22	0.00	0.31	0.00
<b>GY</b>	0.25	0.25	0.05	0.02	0.45	0.00

DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB (g/m<sup>2</sup>) = shoot biomass and GY (g/m<sup>2</sup>) = grain yield

The PCA was visualized using a biplot based on the first two PCs (Figures 1.3 and 1.4). The first two PCs explained 37.3% of the variation exhibited under optimal conditions (Figure 1.3). The progeny exhibited higher SB, TKW, and GY than their parents under optimal conditions. In contrast, the parents exhibited a tendency to attain higher values for TN and DTH, whereas the PH was almost similar under optimal conditions. The first PC explained 19.9% of the variation and was positively associated with PH, SB, and GY while being negatively associated with DTH. The second PC, which accounted for 18.4% of the variation under optimal conditions, was highly associated with TN, TKW, and KPS. In comparison, the first two PCs explained 45.08% of the variation exhibited under drought conditions (Figure 1.4). The progeny exhibited a tendency to be taller and attained higher KPS and TKW than the parents under drought conditions. In contrast, the parents exhibited higher SB and GY than the progeny under drought conditions. The first PC

explained 29.6% of the variation and was associated with KPS, PH, and TKW. whereas the second PC with 15.4% of the variation was correlated to DTH, TN, SB, and GY. The progeny showed a stronger association with the first PC whereas the parents were closely related to PC2.

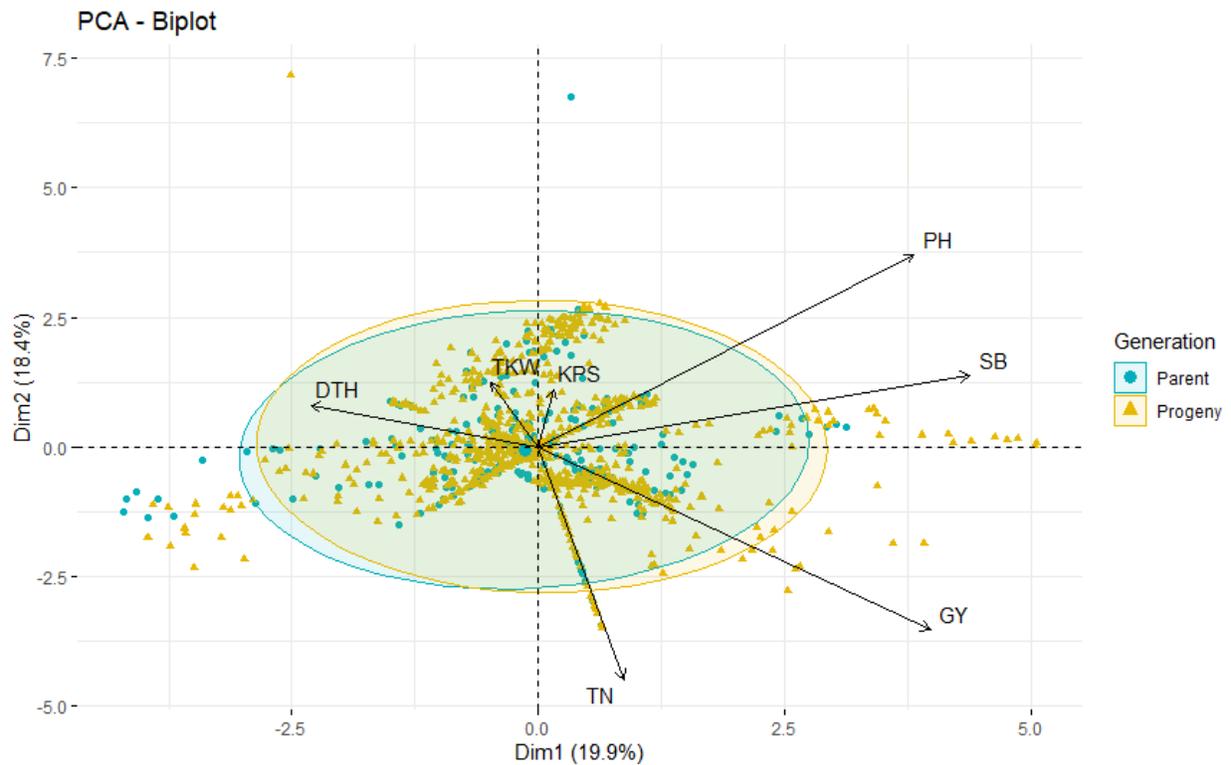


Figure 1.3. Principal component biplot showing relationships among agronomic and yield related traits in wheat under optimum conditions based on 40 studies. Dim1 = principal component 1 (PC1), Dim2 = principal component 2 (PC2), DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB ( $\text{gm}^{-2}$ ) = shoot biomass and GY ( $\text{gm}^{-2}$ ) = grain yield

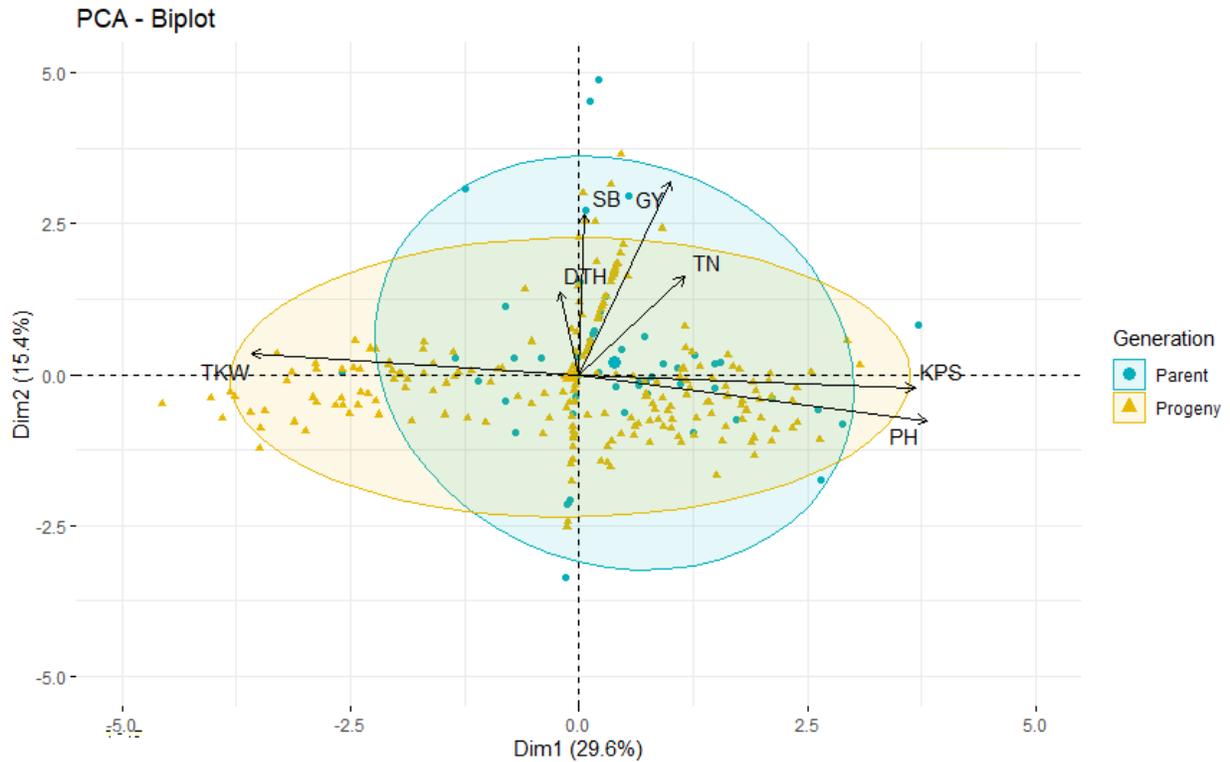


Figure 1.4. Principal component biplot showing relationships among agronomic and yield related traits under drought conditions based on 40 studies. Dim1 = principal component 1 (PC1), Dim2 = principal component 2 (PC2), DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB ( $\text{gm}^{-2}$ ) = shoot biomass and GY ( $\text{gm}^{-2}$ ) = grain yield

### 1.3.3 Effect of drought stress on yield-related traits and relative performance of progeny

Overall, drought stress had significant and negative effects on all traits (Figure 1.5). The effect of drought stress was most pronounced and severe on DTH (with  $-4.5$  effect size), whereas the least effect was observed for KPS ( $-1.25$ ). The effects of drought stress were higher on SB with a value of  $-2.0$  compared to  $-1.30$  for GY. Traits such as KPS, TN, and PH were affected almost equally by drought stress with negative values varying between  $-1.5$  and  $-1.0$ . The comparison of progeny to parental performance showed that the progeny attained significantly higher mean values for traits such as PH, KPS, SB, TN, and DTH (Figure 1.6). The highest positive effects on PH were attained in the progeny versus parents, whereas TKW and GY exhibited no significant differences in performances between progeny and parents.

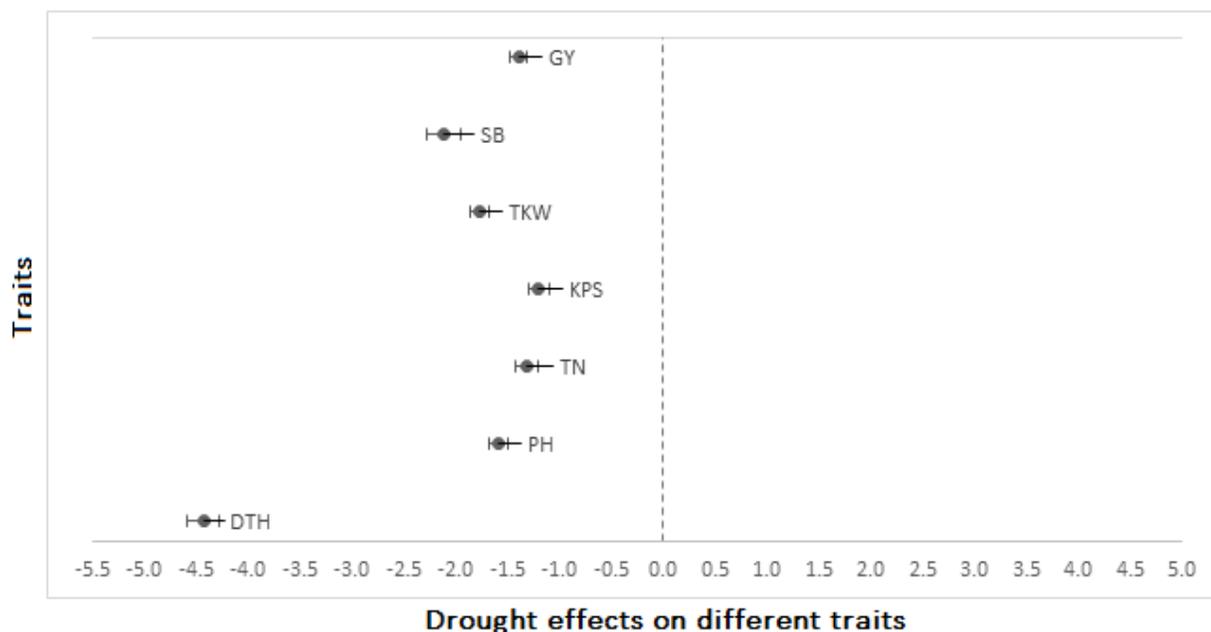


Figure 1.5. Comparison of drought effects on agronomic traits of all wheat genotypes measured based on 40 studies. DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB ( $\text{gm}^{-2}$ ) = shoot biomass and GY ( $\text{gm}^{-2}$ ) = grain yield

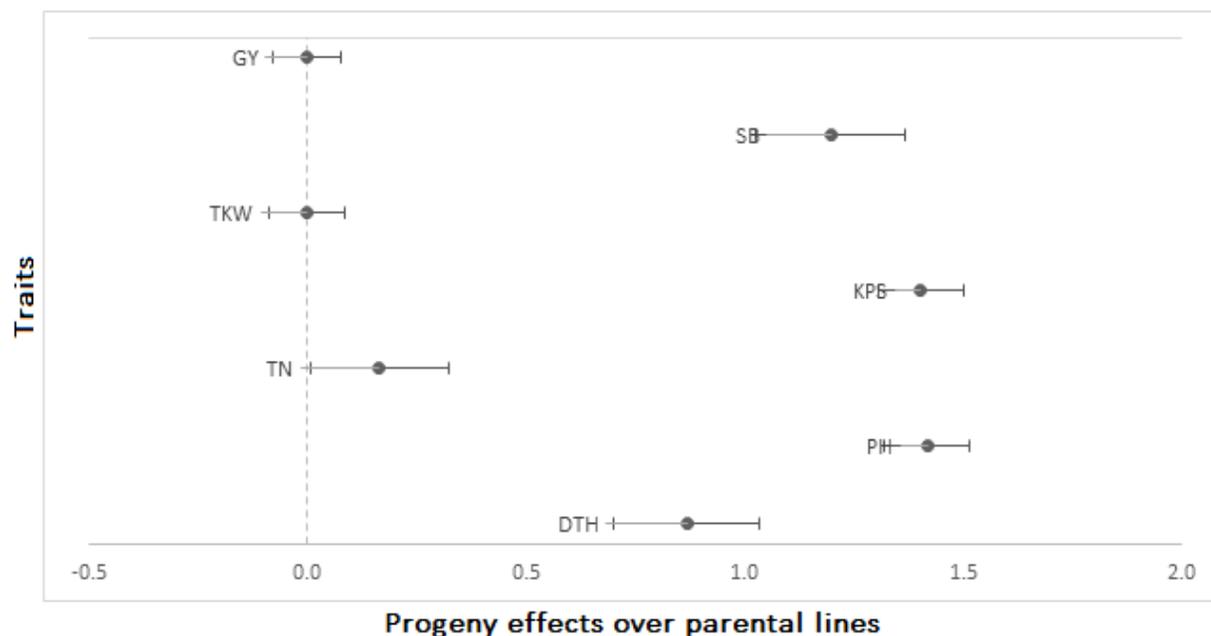


Figure 1.6. Progeny performance in different agronomic and yield related traits compared to parental performance based on 40 studies. DTH = days to heading, PH (cm) = plant height, TN (tillers) = number of tillers per plant, KPS (kernels) = kernels per spike, TKW (g) = thousand kernel weight, SB ( $\text{gm}^{-2}$ ) = shoot biomass and GY ( $\text{gm}^{-2}$ ) = grain yield

## **1.4 Discussion**

### **1.4.1 Distribution and variation of agronomic traits**

The genotypes exhibited wide variation in trait performance across the different water regimes indicating that there was potentially wide genetic diversity in the wheat gene pool for crop improvement (Table 1.2). However, days to heading and PH exhibited the lowest coefficient of variation, which indicate that these traits did not vary widely among the progeny and parents across the different water regimes. Over the last 40 years, there have been concerted efforts to introgress reduced height (Rht) or dwarfing genes into modern cultivars (Würschum, et al., 2017). The Rht genes could potentially have contributed to reduced variation in PH among the genotypes across the different studies examined. Similarly, Chairi, et al. (2018) found that there were nonsignificant differences in PH among durum wheat cultivars released from 1980 to 2008. Reduced PH has been a target trait during breeding as it is envisaged that it increases resource allocation to reproductive traits for attaining higher GY, which is the primary objective of plant breeding programs. However, reduced PH may indirectly reduce carbon sequestration by potentially reducing straw yields that could be incorporated into the soil profile (Aubinet et al., 2009; Jimenez-Berni et al., 2018).

The tillering capacity varied widely reflecting the wide genetic variation that could be exploited for TN. The TN has generally decreased over the years with more emphasis on developing cultivars with a low number of highly productive tillers (Loss and Siddique, 1994; Naruoka et al., 2011). Usually, high biomass accumulation in taller plants with more tillers could lead to higher sequestration of carbon in the soil.

Grain yield was highly variable under different moisture regimes and environments because of its sensitivity to different growing conditions as reflected by its high coefficient of variation. The high variability in GY among the genotypes and between the water regimes reflects the efforts dedicated to breeding for high GY. Grain yield is the primary target for many breeding programs, and the extent of improvement is dependent on available genetic variation, selection efficiency, and the prevailing environmental conditions during selection (Ehdaie et al., 2008; Shamuyarira et al., 2019b). As a quantitative trait, GY is highly variable across genotypes and environments and is mostly selected for indirectly through related secondary traits especially when selecting under stress conditions. The selection efficiency will determine the extent of improvement in GY and

thus the variation observed shows that selection efficiency varied significantly when using different germplasm under different water regimes.

#### **1.4.2 Variation in parental and progeny means for agronomic traits under drought stressed and non-stressed conditions**

In this study, progeny heading time was earlier than that observed in parents suggesting that most breeding focused on developing early flowering genotypes. In most breeding programs, genotypes that flower and mature earlier are selected for developing crosses, and genetic gain is calculated as a reduction in flowering or maturity period leading to earliness in modern cultivars. Rezaei et al. (2018) observed a reduction of between 11 and 14 days in heading time in new winter wheat cultivars compared to the old cultivars that were released between 1950 and 2006. Breeding for earliness in recent years has been necessitated by the need to escape drought in drought-prone environments due to climate change (Shavrukov et al., 2017).

Earlier heading under drought conditions was more expected since drought stress induces accelerated development in plants to complete their life cycle within the shortest possible time as a survival mechanism. However, early heading under optimum conditions has been reported to be disadvantageous on yield potential (Ali, 2011). Under optimum conditions, genotypes that flower and mature earlier fail to maximize the use of the available moisture leading to lower yield attainment than late flowering and maturing genotypes. The high SCA effects under optimum than drought conditions suggest that there is higher expression of favourable nonadditive gene effects when water availability is conducive (Ertiro et al., 2017).

The higher average height observed for progenies than parents under optimum conditions could be due to higher efficiency in resource utilization for biomass production by the progenies. Under optimal conditions, taller progenies with higher biomass have been selected because when resources are not limiting, PH is positively linked to high GY (Mwadzingeni et al., 2016). Alternatively, the lack of differences in PH under drought stress is caused by the negative effect of water stress on plant growth. Water stress is known to reduce cell expansion and growth in plants (Sarto et al., 2017).

The lower TN observed under drought stress could be a drought response mechanism to reduce competition for resources. Blum et al. (1990) noted that tiller development is highly sensitive to drought stress and stops when leaf water potential decreases below  $-2.6$  MPa. However, plants

can recover and initiate tiller development if favourable moisture conditions return after a period of stress.

The similarity in KPS for parents and progenies under both moisture conditions could be attributable to targeted breeding for increased kernel number. Yield gains that have been achieved in wheat elite lines after the green revolution have been attributed to an increase in grain number per unit area which is a function of KPS (Shearman et al., 2005; Yao et al., 2019). This trend could be exploited under drought where the high GCA variation could allow exploitation of additive gene effects to improve grain number under drought conditions. This study revealed that greater improvement of kernel weight can be achieved, and genotypes can be selected for higher partitioning of limited assimilates under drought conditions. Targeting TKW can improve yield effectively under drought compared to optimum by exploiting both additive and nonadditive gene action. Kernel weight has historically contributed little to yield improvement due to the negative effect of Rht genes present in many elite lines to reduce PH (Zhang et al., 2013; Xu et al., 2017, 2019). Thus, it represents untapped opportunity for yield improvement (Daba et al., 2018) especially under drought where the advantages of Rht genes are limited.

Higher SB and GY accumulation under optimal compared to drought stress conditions reflect the increased potential for genetic expression of certain traits when soil moisture is not limiting (Salehi et al., 2014). However, drought severely decreased SB and GY showing that biomass production is highly sensitive to moisture stress through its impact on cell development and reproductive growth (Epie and Maral, 2018; Figuero-Bustos et al., 2019). Higher genetic potential for biomass production is attained as resources become available, and soil moisture is one of the most critical resources for plant growth and biomass production. In addition to reduced productivity, drought stress negatively affects heritability of traits as exhibited by the lower GCA and SCA effects for SB and GY under drought stress. Therefore, selection for SB and GY will be more efficient under optimum conditions where the confounding effects of drought stress are minimal. The confounding effects of drought stress have contributed to slow progress in improving yield performance under drought conditions (Manes et al., 2012). However, the attainment of higher GY by progeny under drought shows that selection has improved drought tolerance among progeny compared to parents.

The higher magnitude of the GCA effects under optimum versus drought conditions for most assessed traits suggests that drought response is under the influence of genotype and genotype ×

environment interaction effects influencing trait heritability (Menezes et al., 2022). Drought restricts the expression of polygenes and their transmission from parents to the offspring hindering selection response which is correlated with the low GCA and SCA values.

#### **1.4.3 Relationship among yield related traits under different moisture regimes**

Relationships among yield related traits are important to facilitate concurrent selection of important traits and allow indirect selection of complex traits such as GY and biomass allocation. The positive correlations between GY and SB under both moisture conditions show that genotypes with higher SB are most likely able to accumulate high GY. Shoot biomass is linked to large canopies for radiation capture and support for increased photosynthetic active area, which are the basis for high reproductive capacity. Shoot biomass could be a reliable trait for improving GY as it also had positive associations with other traits in this study under optimum conditions. In recent years, breeders have been aiming to increase SB while maintaining a high harvest index to drive yield improvement (Jimenez-Berni, et al., 2018). This could also be exploited under drought conditions as highlighted by Shamuyarira et al., (2019a) who observed high aboveground biomass in high yielding drought tolerant genotypes. Furthermore, Gupta et al. (2011) stated that drought tolerant wheat is more efficient in translocating stem reserves from SB to reproductive organs than drought sensitive genotypes. Shoot biomass could be improved simultaneously with PH due to their strong correlation. Similarly, PH has been used as a proxy trait for increasing aboveground biomass in other cereal crops such as maize (*Zea mays* L.) (Yin et al., 2011), barley (*Hordeum vulgare*) (Bendig et al., 2014) and rice (*Oryza sativa*) (Tilly et al., 2015). In addition, TN and KPS will also be useful for increasing GY. Zhao et al. (2020) highlighted the positive contribution of TN to GY. However, this is only advantageous under drought conditions if the increased TN manage to produce spikes that will contribute to yield gain (Mwadzingeni et al., 2018). The positive correlation of GY with KPS was expected as increase in kernel number is a major contributor to GY (Fischer, 2008). On the other hand, the negative association of TKW with PH, TN, and KPS under drought could be a result of weak source strength due to low photosynthetic activity and carbon assimilation (Fisher, 2008; Saeidi and Abdoli, 2015). This could lead to competition for the limited available assimilates resulting in shrivelled grains with low grain weight and complicate the selection process for multiple trait improvement.

The PCA revealed that DTH, PH, TN, SB, and GY were the major contributors to the variation explained by the first three components under both optimum and drought-stressed conditions. The concurrent selection of these traits could lead to improved productivity under different conditions of moisture availability. Notably, PH had high positive loadings on the first PCs under both water regimes showing that it could be the most important trait for selection to exploit response to breeding and water availability. Mo et al. (2018) highlighted the importance of manipulating PH as the major contribution to yield gains achieved during the green revolution. Kernels per spike contributed highly on the first PC under drought but its contribution under optimum conditions was low, suggesting that KPS was more important for discriminating between genotypes under drought stress.

The PC biplots revealed higher SB and TKW for progeny than parents, indicating an increase in genetic gains for these traits under optimum conditions which corroborates reports by Wu et al. (2014) and Yao et al. (2019). In contrast, the parents attained higher values for TN than the progeny suggesting that breeders have selected for reduced TN in successive generations. Under drought conditions, progenies were characterized by high PH, KPS, and TKW than the parents. This suggests that there were genetic gains achieved in PH, kernel number, and kernel weight under drought on the materials that were used in this study. However, parents seemed to have higher SB and GY under stress. This could be because most selection programs happen under optimal conditions, thus the crosses selected are usually adapted for high input and nonstress conditions. In such cases, drought-stress masks the impact of a high number of genes that contribute to crop vigor which could lead to poor performance in drought susceptible genotypes (Nezhadahmadi et al., 2013).

#### **1.4.4 Drought effects and progeny performance in yield related traits**

A meta-analysis was conducted on the quantitative data to compare the effect sizes of drought and crossing on biomass allocation and yield related traits in different studies. The biggest effect of drought stress were on DTH and SB, which is concomitant with accelerated phenological development and reduced plant productivity normally associated with lack of soil moisture. Drought is known to reduce the duration to flowering in wheat as mechanism of drought escape. However, early flowering and maturity reduces the entire growth cycle of a plant and may lead to limited capacity to accumulate SB (Fábián et al., 2019). In cases where SB is severely affected,

the plant may lack the requisite vegetative stature to support full genetic potential for reproductive growth leading to poor yield formation. However, Shavrukov et al. (2017) argues that there are instances when early heading can be exploited to increase productivity especially in hotter environments that may allow faster SB production. Early flowering and maturity are critical traits in Sub-Saharan Africa where climate change is projected to increase temperature and reduce precipitation. The small impact of drought on KPS and its high progeny effects indicate the stability of kernel number under varying moisture regimes compared to all the other traits. Therefore, continued exploitation of KPS could lead to successful development of drought tolerant cultivars with high kernel numbers under drought. Fábíán et al. (2011) identified lower seed set as the major cause of yield loss under drought.

The high effects sizes of drought stress on DTH and SB show that these traits were more sensitive to drought stress than the other traits. Differences in sensitivity of traits to drought have been reported previously. For instance, SB was reported to be more sensitive to drought compared to other traits such as root biomass, KPS, and grain weight (Ehdaie et al., 2008; Mathew et al., 2019b; Shamuyarira, et al., 2019a). The high sensitivity of SB is due to cumulative effects of the other traits since SB is an aggregate product of the association among secondary traits.

The higher mean values for traits such as PH, KPS, SB, TN, and DTH in progeny than in parents suggest that there could be transgressive segregants. The possibility of generating transgressive segregants during crossing is highly dependent on the choice of parental genotypes used in making crosses (Kuczyńska et al., 2007). Selection of divergent parental lines in crossing promotes new gene recombination that improve traits beyond their initial genetic variation. Thus, it is envisaged that crossing parental lines with divergent rooting characteristics could produce transgressive segregants for improved rooting ability and biomass allocation.

### **1.5 Implications for breeding for biomass allocation**

The results of this meta-analysis revealed that there is sufficient variation for above ground traits to improve productivity and possibly biomass allocation in wheat for food production and ecosystem services such as nutrient recycling and carbon retention. The positive GCA and SCA effects for SB show that there is potential for improvement in SB production and this also provides evidence for possibility of altering biomass allocation in wheat. Since shoot and root biomass possibly share some common loci (Mathew et al., 2019a), the evidence for GCA and SCA effects

for SB show that root biomass could also be improved using similar strategies for SB. This could be utilised in estimating possible genetic gains that could be achieved in enhancing belowground biomass allocation. Secondary traits have been used extensively to select for GY and can also be adopted for biomass allocation of the total plant phenotype. Belowground biomass partitioning has long been neglected despite the potential wide genetic variation that could be exploited to improve wheat performance under varying environments (Lynch, 2007). With climate change, it will be essential to optimize total biomass allocation to withstand the adverse effects of drought while simultaneously maintaining soil health by retention of biomass for carbon sequestration. Therefore, there is a need to explore root biomass traits together with aboveground biomass traits and establish models that will facilitate easier prediction or estimation of root biomass from above ground traits. Models that allow estimation of root biomass traits have become increasingly imperative to proffer carbon budget estimations and development of climate smart cultivars for mitigating climate change impact.

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Appendix 1.1: References included in the database including replications, experiments, environments, traits collected in the study and the country in which the studies were conducted

<b>No.</b>	<b>Author</b>	<b>Rep</b>	<b>Exp</b>	<b>Env</b>	<b>Mating design</b>	<b>Data considered from study</b>	<b>Country</b>
1	Abdallah et al 2015	3	1	Field	Half-diallel	DTH, DTM, PH, KPS, TKW, GY	Egypt
2	Adel and Ali 2013	3	1	Field	Half-diallel	DTH, PH, TN, GY	Libya
3	Ahmad et al 2013	3	1	Field	Half-diallel	DTH, DTM, PH, GY	Pakistan
4	Akinci 2009	4	1	Field	Half-diallel	DTH, TKW, GY	Turkey
5	Hama Amin et al 2019	3	2	Field	Full-diallel	SB, KPS, TKW, GY	Iraq
6	Bibi et al 2013	3	1	Field	Line x tester	KPS, GY	Pakistan
7	Brahim et al 2014	3	1	Field	Full-diallel	PH, KPS, TKW	Algeria
8	El-Hosary et al 2012	3	2	Field	Half-diallel	GY	Egypt
9	El-Rawy et al 2018	3	1	Field	Half-diallel	TKW, GY	Egypt
10	Fellahi et al 2013	3	1	Field	Line x tester	DTH, PH, TN, KPS, TKW, GY	Algeria
11	Golparvar et al 2014	3	1	Field	Half diallel	SB	Iran
12	Hassan et al 2018	3	1	Field	Half-diallel	DTH, DTM, PH, KPS, TKW, GY	Egypt
13	Ijaz et al 2017	3	1	Field	Line x tester	PH, TN, KPS, GY	Pakistan
14	Iqbal et al 2007	4	2	Field	Half-diallel	GY	Canada
15	Ishaq et al 2018	3	1	Field	Line x tester	SB, DTH, DTM, GY	Pakistan
16	Istipliler et al 2015	3	1	Field	Line x tester	PH, TKW, GY	Turkey
17	Joshi et al 2004	3	1	Field	Half-diallel	GY	India
18	Khaled et al 2013	3	1	Field	Half-diallel	DTH, GY	Egypt
19	Khokhar et al 2019	3	1	Field	Half-diallel	DTH, DTM, PH, TKW, GY	Pakistan
20	Kumar et al 2011	3	1	Field	Half-diallel	PH, TN, KPS, TKW, GY	India
21	Kumar et al 2017	3	1	Field	Half-diallel	SB, DTH, TN, GY	India
22	Li et al 1997	3	1	Field	Line x tester	PH	China
23	Motawea et al 2017a	3	1	Field	Half-diallel	DTH, TKW, GY	Egypt
24	Motawea et al 2017b	3	1	Field	Half-diallel	SB, PH,TKW, GY	Egypt
25	Mwadzingeni et al 2018	2	2	Field/GH	Half-diallel	PH, TN, KPS, TKW, GY	South Africa
26	Nazir et al 2005	3	1	Field	Full-diallel	TN, KPS, TKW, GY	Pakistan
27	Nornberg et al 2016	3	1	Field	Half-diallel	GY	Brazil

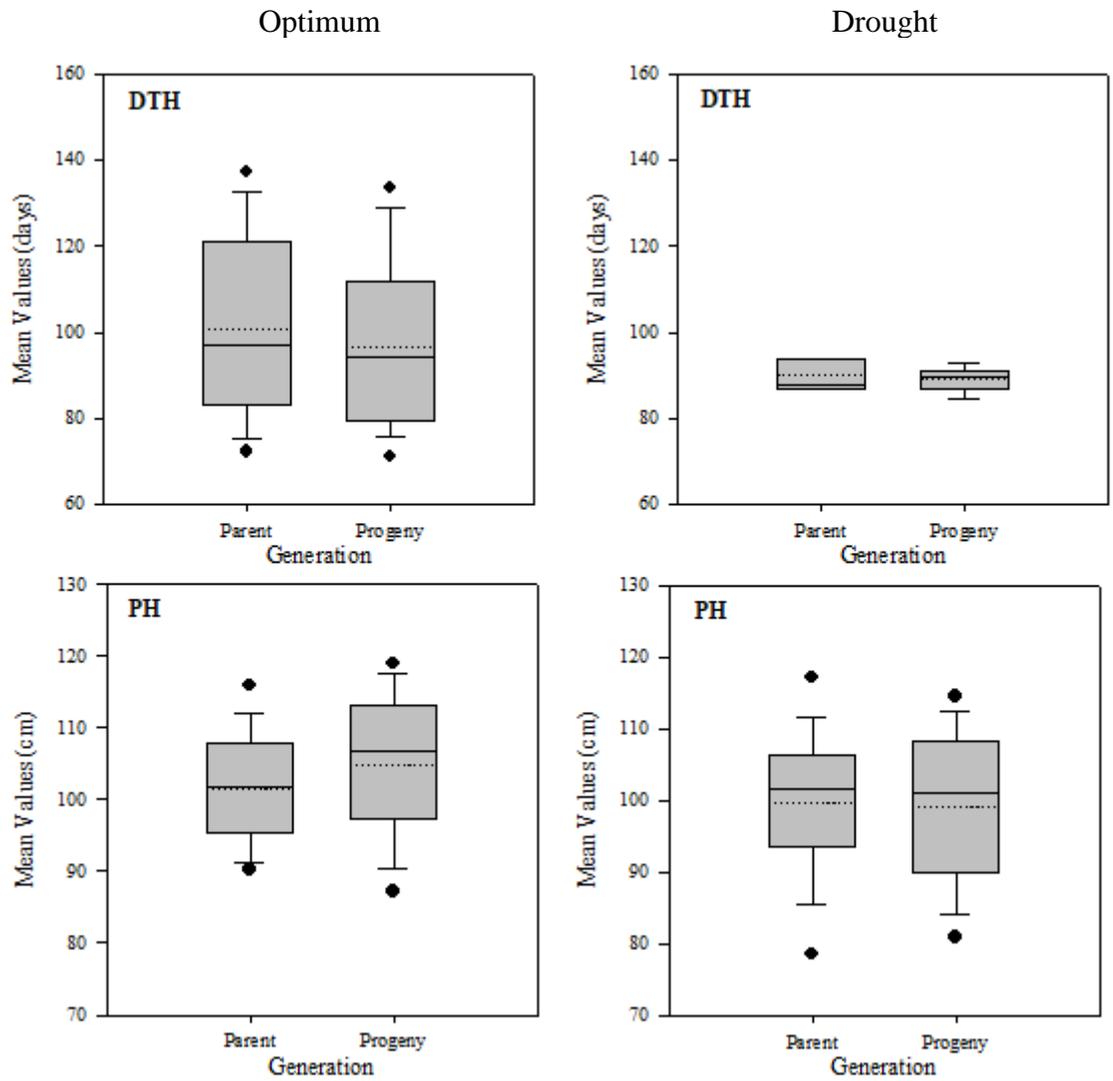
<b>No.</b>	<b>Author</b>	<b>Rep</b>	<b>Exp</b>	<b>Env</b>	<b>Mating design</b>	<b>Data considered from study</b>	<b>Country</b>
28	Pagliosa et al 2017	3	1	Field	Half-diallel	GY	Brazil
29	Qabil N. 2017	3	1	Field	Half-diallel	DTH, KPS, TKW, GY	Egypt
30	Saeed et al 2016	3	1	Field	Line x tester	TN, KPS, TKW, GY	Pakistan
31	Salehi et al 2014	3	1	Field	Half-diallel	SB, GY	Iran
32	Shaban et al 2018	3	1	Field	Half-diallel	DTH, DTM, TKW, GY	Egypt
33	Shah et al 2018	3	1	Field	Line x tester	SB, TN, TKW, GY	India
34	Singh et al 1969	4	1	Field	Half-diallel	TKW, GY	India
35	Singh et al 2012	3	2	Field	Half-diallel	SB, DTM, PH, TN, KPS, GY	India
36	Tayade et al 2019	3	1	Field	Half-diallel	DTM, PH, TN, KPS, TKW, GY	India
37	Topal et al 2004	3	1	Field	Full-diallel	TKW, GY	Turkey
38	Valerio et al 2009	3	1	Field	Half-diallel	TN, KPS, GY	Brazil
39	Yao et al 2011	3	1	Field	Half-diallel	PH	China
40	Zare-kohan and Heidari 2012	3	2	Field	Half-diallel	PH, GY	Iran

Rep = replications, Exp = experiments, Env = environments, GH = greenhouse, DTH = days to heading, PH (cm) = plant height, TN = number of tillers per plant, KPS = kernels per spike, TKW (g) = thousand kernel weight, SB (g/m<sup>2</sup>) = shoot biomass and GY (g/m<sup>2</sup>) = grain yield

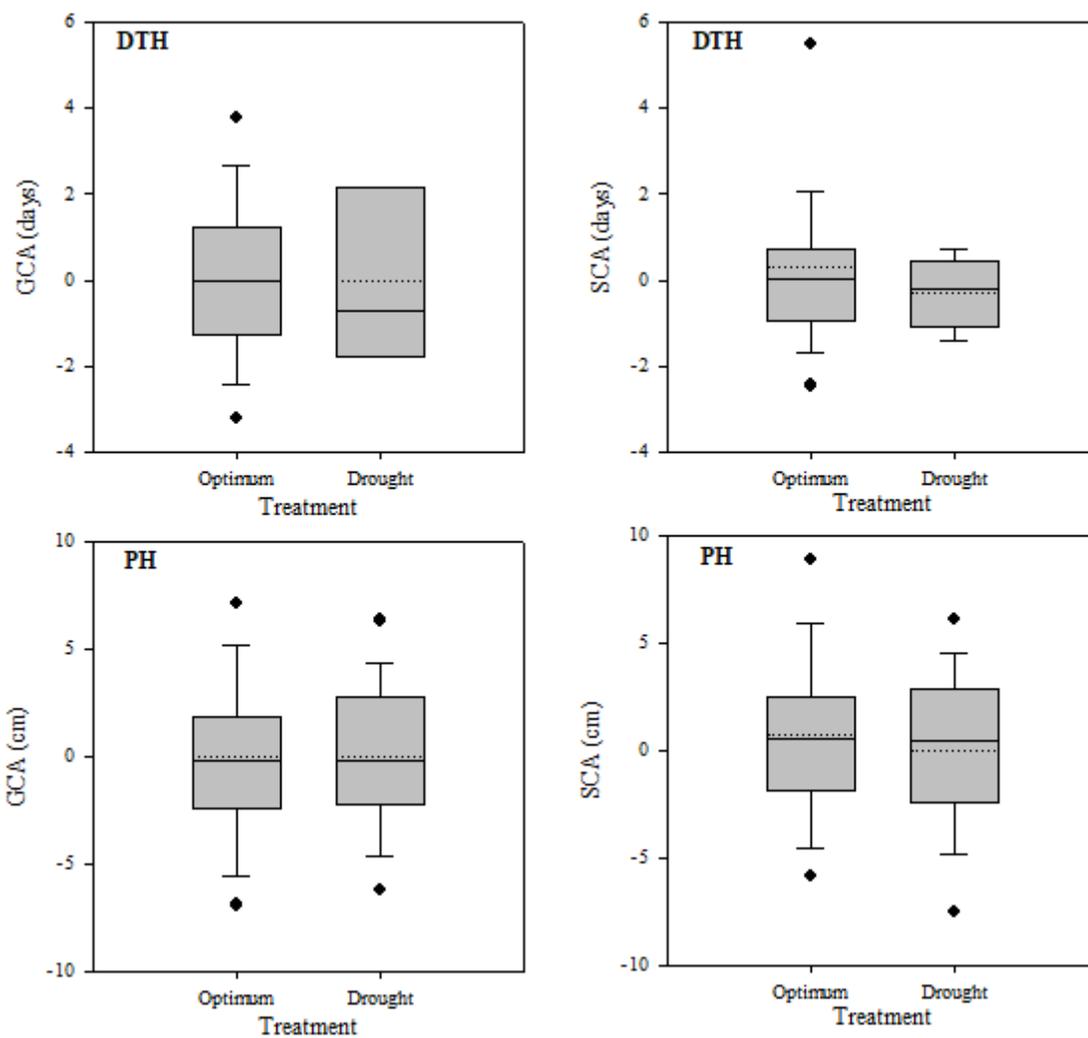
## Appendix 1.2: Links to references used in the database

No.	Author	Link to study
1	Abdallah et al 2015	<a href="http://www.publications.zu.edu.eg/Pages/PubShow.aspx?ID=26776&amp;&amp;pubID=18">http://www.publications.zu.edu.eg/Pages/PubShow.aspx?ID=26776&amp;&amp;pubID=18</a>
2	Adel and Ali 2013	<a href="https://doi.org/10.3923/ajcs.2013.14.23">https://doi.org/10.3923/ajcs.2013.14.23</a>
3	Ahmad et al 2013	<a href="http://www.aup.edu.pk/sj_pdf/003%20article%20233-2010%20(COMBINING%20ABILITY%20EFFECTS).pdf">http://www.aup.edu.pk/sj_pdf/003%20article%20233-2010%20(COMBINING%20ABILITY%20EFFECTS).pdf</a>
4	Akinci 2009	<a href="http://www.agrojournal.org/15/03-05-09.pdf">http://www.agrojournal.org/15/03-05-09.pdf</a>
5	Hama Amin et al 2019	<a href="http://dx.doi.org/10.15666/aeer/1702_30133032">http://dx.doi.org/10.15666/aeer/1702_30133032</a>
6	Bibi et al 2013	<a href="https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.1074.8283&amp;rep=rep1&amp;type=pdf">https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.1074.8283&amp;rep=rep1&amp;type=pdf</a>
7	Brahim et al 2014	<a href="https://academicjournals.org/journal/AJB/article-abstract/E97B0A242696">https://academicjournals.org/journal/AJB/article-abstract/E97B0A242696</a>
8	El-Hosary et al 2012	<a href="https://www.bu.edu.eg/portal/uploads/Agriculture/Agronomy/1124/publications/Mahmoud%20El-Zaabalawy%20Mahmoud%20El-Badawy_elhosary%20and%20badawy.pdf">https://www.bu.edu.eg/portal/uploads/Agriculture/Agronomy/1124/publications/Mahmoud%20El-Zaabalawy%20Mahmoud%20El-Badawy_elhosary%20and%20badawy.pdf</a>
9	El-Rawy et al 2018	<a href="https://doi.org/10.9787/PBB.2018.6.3.206">https://doi.org/10.9787/PBB.2018.6.3.206</a>
10	Fellahi et al 2013	<a href="https://doi.org/10.1155/2018/8312857">https://doi.org/10.1155/2018/8312857</a>
11	Golparvar et al 2014	<a href="https://doi.org/10.2298/GENSR1401043G">https://doi.org/10.2298/GENSR1401043G</a>
12	Hassan et al 2018	<a href="https://doi.org/10.21608/ajs.2018.28289">https://doi.org/10.21608/ajs.2018.28289</a>
13	Ijaz et al 2017	<a href="https://apply.jar.punjab.gov.pk/upload/1502446372_127_1_581.pdf">https://apply.jar.punjab.gov.pk/upload/1502446372_127_1_581.pdf</a>
14	Iqbal et al 2007	<a href="https://doi.org/10.1007/s10681-006-9289-y">https://doi.org/10.1007/s10681-006-9289-y</a>
15	Ishaq et al 2018	<a href="http://dx.doi.org/10.19045/bspab.2018.70019">http://dx.doi.org/10.19045/bspab.2018.70019</a>
16	Istipliler et al 2015	<a href="https://dergipark.org.tr/en/pub/tjfc/issue/17157/179352">https://dergipark.org.tr/en/pub/tjfc/issue/17157/179352</a>
17	Joshi et al 2004	<a href="https://doi.org/10.1111/j.1601-5223.2004.01730.x">https://doi.org/10.1111/j.1601-5223.2004.01730.x</a>
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19	Khokhar et al 2019	<a href="http://dx.doi.org/10.19045/bspab.2019.80142">http://dx.doi.org/10.19045/bspab.2019.80142</a>
20	Kumar et al 2011	<a href="https://academicjournals.org/journal/JPBCS/article-abstract/3DF052E9389">https://academicjournals.org/journal/JPBCS/article-abstract/3DF052E9389</a>
21	Kumar et al 2017	<a href="https://doi.org/10.20546/ijcmas.2017.612.161">https://doi.org/10.20546/ijcmas.2017.612.161</a>
22	Li et al 1997	<a href="https://doi.org/10.1023/A:1003092432309">https://doi.org/10.1023/A:1003092432309</a>
23	Motawea et al 2017a	<a href="https://doi.org/10.21608/JPP.2017.40552">https://doi.org/10.21608/JPP.2017.40552</a>
24	Motawea et al 2017b	<a href="https://doi.org/10.21608/jpp.2017.42006">https://doi.org/10.21608/jpp.2017.42006</a>
25	Mwadzingeni et al 2018	<a href="https://doi.org/10.1111/pbr.12609">https://doi.org/10.1111/pbr.12609</a>
26	Nazir et al 2005	<a href="https://portal.issn.org/resource/ISSN/1814-960X">https://portal.issn.org/resource/ISSN/1814-960X</a>
27	Nornberg et al 2016	<a href="http://www.cropj.com/nornberg_10_7_2016_977_984.pdf">http://www.cropj.com/nornberg_10_7_2016_977_984.pdf</a>

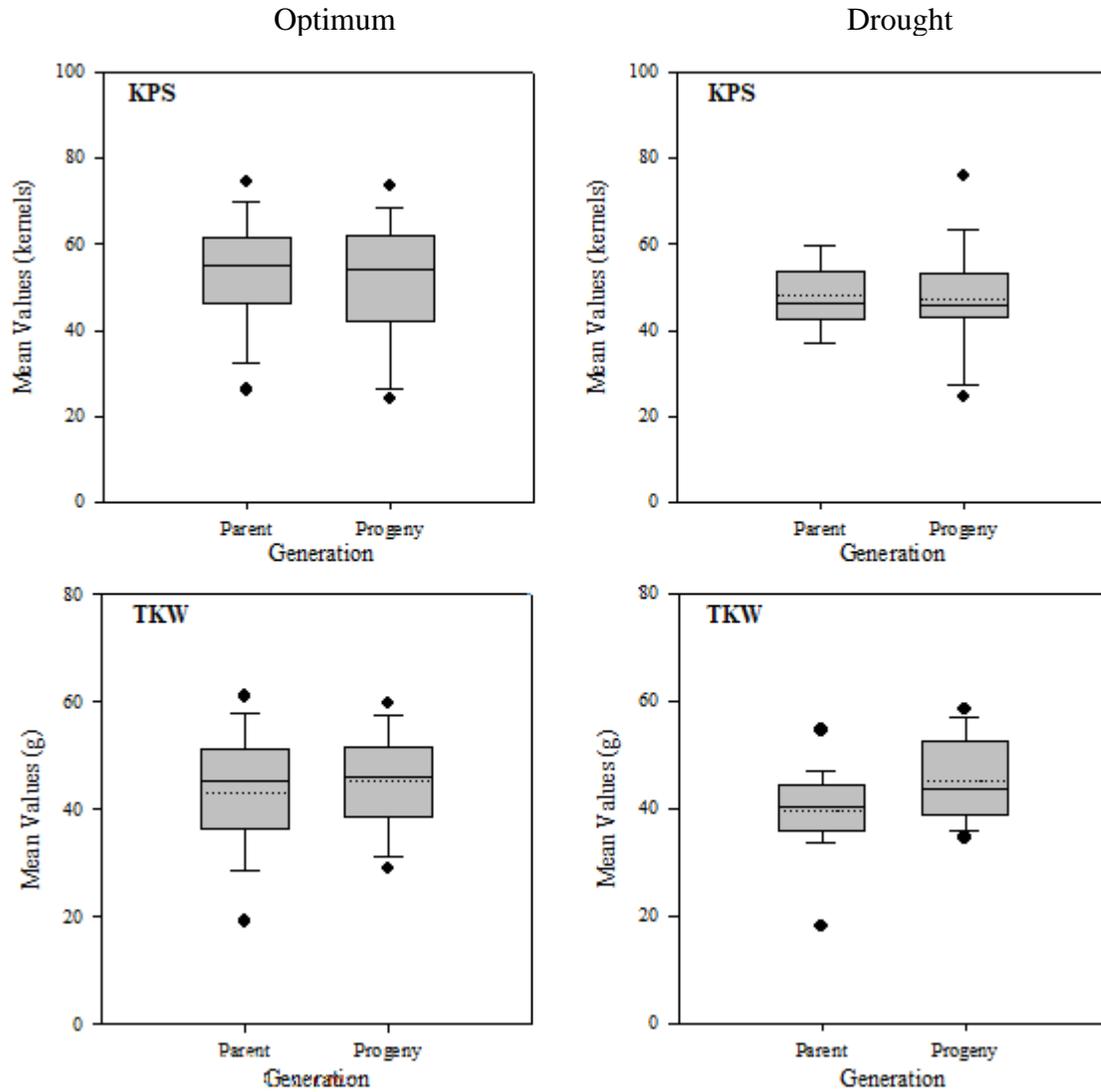
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28	Pagliosa et al 2017	<a href="https://doi.org/10.21475/AJCS.2017.11.01.289">https://doi.org/10.21475/AJCS.2017.11.01.289</a>
29	Qabil N. 2017	<a href="https://dx.doi.org/10.21608/agro.2017.1388.1069">https://dx.doi.org/10.21608/agro.2017.1388.1069</a>
30	Saeed et al 2016	<a href="https://doi.org/10.21162/PAKJAS%2F16.2036">https://doi.org/10.21162/PAKJAS%2F16.2036</a>
31	Salehi et al 2014	<a href="https://hrcak.srce.hr/136727">https://hrcak.srce.hr/136727</a>
32	Shaban et al 2018	<a href="https://dx.doi.org/10.21608/zjar.2018.48407">https://dx.doi.org/10.21608/zjar.2018.48407</a>
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34	Singh et al 1969	<a href="https://doi.org/10.1266/jjg.44.367">https://doi.org/10.1266/jjg.44.367</a>
35	Singh et al 2012	<a href="https://www.openaccessjournal.com/journal/104/Indian-journal-of-agricultural-sciences">https://www.openaccessjournal.com/journal/104/Indian-journal-of-agricultural-sciences</a>
36	Tayade et al 2019	<a href="https://www.phytojournal.com/archives/2019/vol8issue6/PartAD/8-6-355-341.pdf">https://www.phytojournal.com/archives/2019/vol8issue6/PartAD/8-6-355-341.pdf</a>
37	Topal et al 2004	<a href="https://doi.org/10.1016/j.fcr.2003.08.015">https://doi.org/10.1016/j.fcr.2003.08.015</a>
38	Valerio et al 2009	<a href="https://publons.com/publon/11683296/">https://publons.com/publon/11683296/</a>
39	Yao et al 2011	<a href="http://www.cropj.com/yao_5_11_2011_1408_1418.pdf">http://www.cropj.com/yao_5_11_2011_1408_1418.pdf</a>
40	Zare-kohan and Heidari 2012	<a href="http://ccsenet.org/journal/index.php/jas/article/view/16282">http://ccsenet.org/journal/index.php/jas/article/view/16282</a>



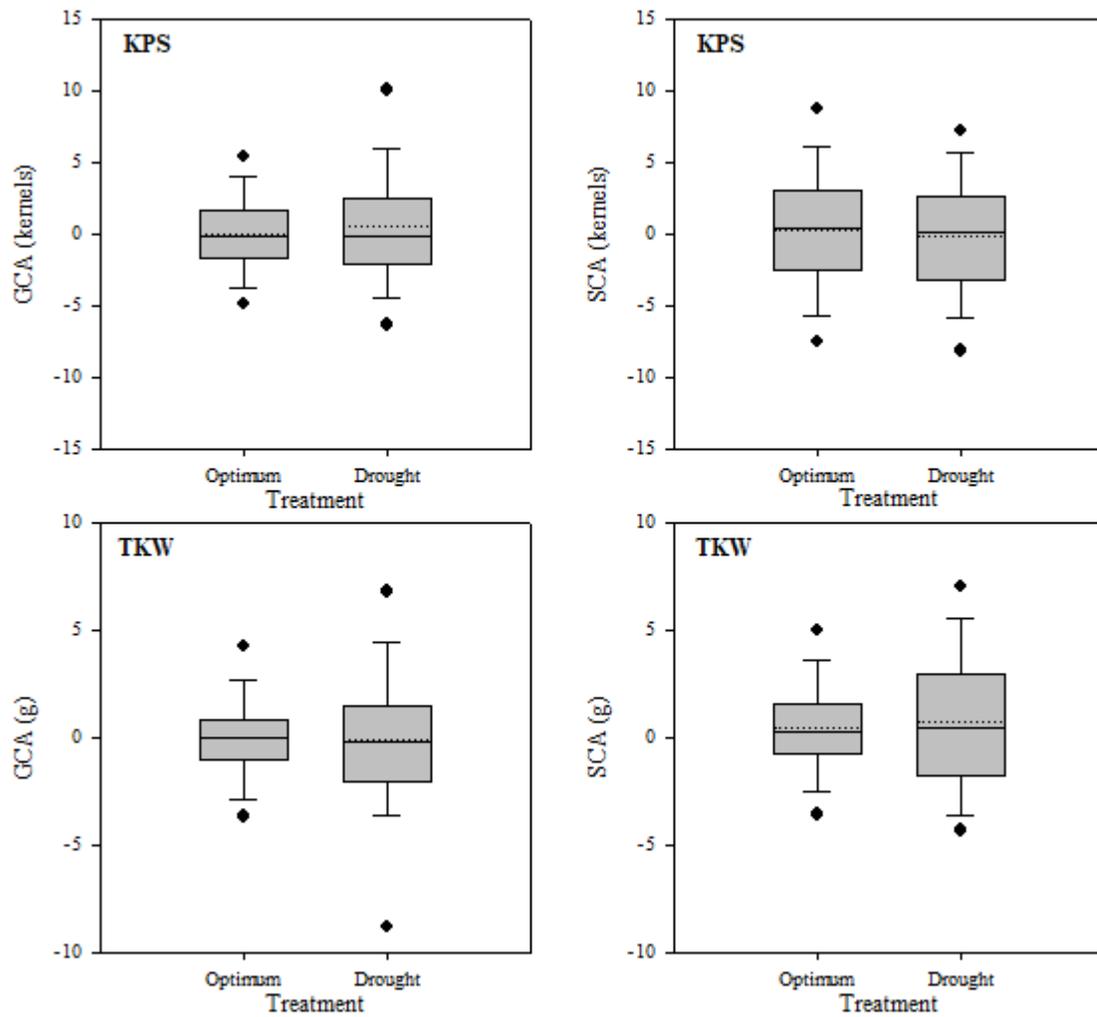
Appendix 1.3. Box plots showing the distribution of mean values for days to heading (DTH) and plant height (PH) under optimum (left side) and drought (right side) conditions



Appendix 1.4. Box plots showing the distribution of general combining ability (GCA) and specific combining ability (SCA) effects for days to heading (DTH) and plant height (PH) under optimum and drought conditions



Appendix 1.5. Box plots showing the distribution of mean values for kernels per spike (KPS) and thousand kernel weight (TKW) under optimum (left side) and drought (right side) conditions



Appendix 1.6. Box plots showing the distribution of general combining ability (GCA) and specific combining ability (SCA) effects for kernels per spike (KPS) and thousand kernel weight (TKW) under optimum and drought conditions

## Chapter 2: Comparative Genetic Diversity Analysis for Biomass Allocation and Drought Tolerance in Wheat (*Triticum aestivum* L.)

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### Abstract

Genetic diversity is invaluable in developing climate-smart and drought-adapted wheat varieties. The aim of this study was to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents. A total of 97 bread wheat genotypes were evaluated in field and greenhouse trials under drought-stressed and non-stressed conditions and genotyped using 16,382 high-density single nucleotide polymorphism (SNP) markers. The analysis of molecular variance showed that the intrapopulation variance was very high at 99%, with a small minimal inter-population variance (1%). The genetic distance, polymorphic information content and expected heterozygosity varied from 0.20 to 0.88, 0.24 to 1.00 and 0.29 to 0.58, respectively. The cluster analysis based on SNP data showed that 44% and 28% of the assessed genotypes maintained their genetic groups compared to hierarchical clusters under drought-stressed and non-stressed phenotypic data, respectively. The joint analysis using genotypic and phenotypic data resolved three heterotic groups and allowed the selection of genotypes BW140, BW152, BW157, BW162, LM30, LM47, LM48, LM52, LM54 and LM70. The selected genotypes were the most genetically divergent, with high root biomass and grain yield and are recommended for production or breeding.

**Keywords:** *Biomass allocation; Bread wheat; Carbon sequestration; Drought-stress; Genetic diversity; Root traits*

## 2.1 Introduction

Wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ , AABBDD) is a globally highly valued commodity crop cultivated on about 216 million hectares and provides some 766 million tonnes of grain annually (FAOSTAT, 2021). In Sub-Saharan Africa (SSA), wheat productivity remains low, with a total production of 7.5 million tonnes accounting for only 1.4% of global wheat production (Tadesse et al., 2019). Wheat production in SSA is predominantly under dryland conditions. The region is exceptionally vulnerable to climate change, with devastating consequences of poor productivity and food insecurity (Yahaya and Shimelis 2022). Climate change-induced abiotic stresses, such as heat, drought and poor soil fertility conditions, are the major cause of low wheat productivity (Zougmore et al., 2018). Pironon et al. (2019) reported that new sources of genes with abiotic stress tolerance, targeted breeding and speed breeding technologies are among the key strategies in increasing the productivity and adaptive capacity of dryland agriculture in SSA. Therefore, ideotype breeding using key above-ground yield influencing traits, root biomass and root-related traits in plant breeding programs will directly increase drought-stress tolerance and resilience of crops.

The root system is a vital part of a plant providing anchorage and support, access and mobilization of water and nutrients and soil carbon sequestration for plant growth and development (Voss-Fels et al., 2018). However, breeding under intensive agronomic management and high input production systems has progressively led to weaker root systems in modern wheat cultivars (Wasson et al., 2012; OlaOlorun et al., 2020). As a result, most modern wheat varieties are highly susceptible to moisture stress, and their weak root system has limited agility to environmental adaptation and access to soil moisture and nutrients (Voss-Fels et al., 2019). Developing new and modern wheat cultivars with optimized biomass allocation and large root systems will enhance adaptation and wheat productivity in dryland farming systems of SSA (Gram et al., 2020).

Breeding for high-yielding varieties with robust root systems requires adequate genetic variation for above-ground agro-morphological traits and root biomass. However, due to difficulties associated with root sampling and phenotyping, a few studies have evaluated genetic variation and selection for root traits in wheat (Junaidi et al., 2018; Nguyen and Stangoulis 2019; Guo et al., 2020; Maeoka et al., 2020; Rufo et al., 2020). Above-ground phenotypic traits such as days to flowering and maturity, tillering ability, plant height and grain yield can be assessed using direct

and simple measurements. However, assessing root attributes such as root biomass, root length and root diameter is laborious and invasive, requiring destructive sampling to access root samples (Paez-Garcia et al., 2015). Understanding the interrelationship between above-ground phenotypic traits and root attributes could allow breeders to manipulate biomass allocation between roots and shoots to create a better crop ideotype with more extensive roots to improve productivity in a wide range of environments (Shamuyarira et al., 2022). For instance, root biomass has been found to be highly correlated with seedling shoot development, water use efficiency and high grain yield (Manschadi et al., 2006; Hammer et al., 2009; Chen et al., 2015; Suneja et al., 2019). Dual selection for increased root biomass and yield gain is dependent on the balance of sink-source between root and reproductive organs (Schultz et al., 2013).

Genetic diversity analysis through phenotypic traits and root attributes is affected by genotype by environment interaction. Crop species have phenotypic plasticity and modify their response due to prevailing environmental conditions (Pieruschka and Schurr 2019). Phenotypic plasticity could limit the efficiency and accuracy of phenotyping (Joshi et al., 2017). Conversely, genomic tools such as genomic selection, genome engineering, genome editing and quantitative trait loci (QTL) analysis have become valuable in crop improvement programs, including wheat (Morgante and Salamini 2003; Boukar et al., 2019; Bohra et al., 2020). Different molecular markers such as random amplified polymorphic DNA (RAPD), simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) markers have been used in genetic diversity studies of wheat (Chen et al., 2012; Rufo et al., 2019; Nazarzadeh et al., 2020). SNP markers have gained prominence in genetic diversity analysis due to wide distribution across the genome, genetic stability, compatibility with automation and ease of genotyping (Mammadov et al., 2012; Chung et al., 2017). These markers are especially suitable for studying the genetic diversity of crops with a large and complex genomic structure, such as wheat (Thomson 2014). Therefore, it is essential to complement phenotypic selection with molecular markers to capture allelic diversity (Agre et al., 2019) and understand the underlying genetic basis and interrelationships with root traits and biomass partitioning.

Optimizing biomass allocation in new wheat cultivars would increase productivity in rain-fed agro-ecologies while concurrently reducing agriculture's carbon footprint (Shamuyarira et al., 2022). Assessing the genetic variation among available wheat germplasm will provide information

useful for classifying wheat genotypes into different genetic groups for combining ability analysis and development of new breeding populations. Therefore, the aim of this study was to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphisms (SNP) markers to select breeding parents.

## **2.2 Materials and methods**

### **2.2.1 Germplasm**

A panel of 97 bread wheat (*T. aestivum* L.) genotypes were used for the study. Ninety-two of the genotypes were obtained from the International Maize and Wheat Improvement Center (CIMMYT) drought and heat tolerant nurseries. The genotypes were selected for their potential drought tolerance and diversity in rooting ability. The remaining five genotypes were locally adapted and widely grown South African lines that were included to serve as checks. The names and pedigrees of the assessed genotypes are presented in Appendix 2.1.

### **2.2.2 Phenotyping trials**

Three separate experiments were conducted under drought-stressed and non-stressed conditions. Two greenhouse trials were carried out at the Controlled Environment Facility (CEF), and one field trial was conducted at the Ukulinga Research Farm (29° 40' S, 30° 24' E) of the University of KwaZulu-Natal (UKZN) in South Africa between 2016 and 2018. The average temperature in the greenhouse was maintained at 25 °C during the day and 15 °C at night and, the humidity was maintained at between 45% to 55% during the experiment. The greenhouse experiments were all laid out in a 10 × 10 alpha lattice design with two replications. Plants were sown in 10 L capacity plastic pots filled with composted pine bark. Eight seeds were initially planted and thinned to five plants per pot after two weeks of growth. Irrigation and fertiliser (Agchem EasyGro Starter, Pietermaritzburg, South Africa and Agchem Easygro Calmag, Pietermaritzburg, South Africa) were applied using an automated drip irrigation system as per recommendation (DAFF 2010). The plants received 3 minute fertigation cycles four times daily to maintain moisture content at 70% of field capacity (FC). Adequate water was supplied for six weeks after emergence before initiating the drought stress treatment accordingly. Drought stress was induced by withholding irrigation until soil water content dropped to 30% FC, and then re-watering to field capacity to allow for continued plant growth and development. The non-stressed treatment received adequate moisture

until maturity. The soil moisture was monitored with a soil moisture probe (GTDSMM500, General Tools and Instruments, Secaucus, NJ, USA).

The field experiment was laid out in a  $10 \times 10$  alpha lattice design with two replications. The soil surface was covered with a custom-made black plastic mulch to exclude infiltration of rainwater in the soil profile. Each genotype was planted on a 0.5 m long row, and the rows were 0.5 m apart. Ten plants per genotype were established equidistant within a row. Nitrogen, phosphorous and potassium were applied at rates of 120, 30 and 30 kg ha<sup>-1</sup>, respectively, at planting as per recommendation (DAFF 2010). Water was supplied by an automated drip irrigation system. For the non-stressed treatment, adequate water was supplied until maturity. Drought stress was induced by withholding irrigation five weeks after emergence in the drought treatment. After that, irrigation was sparingly applied to prevent permanent wilting. Soil moisture was monitored using digital moisture sensors (HOBO UX120, Onset, Bourne, MA, USA).

Data on days to 50% heading (DTH), days to 50% maturity (DTM), plant height expressed in centimeters (PH), tiller number (TN), plant biomass (PB, g m<sup>-2</sup>), shoot biomass (SB, g m<sup>-2</sup>), root biomass (RB, g m<sup>-2</sup>), root-to-shoot ratio (RS) and grain yield (GY, g m<sup>-2</sup>) were recorded from both greenhouse and field trials. Prior to analysis, data from greenhouse and field experiments were standardized by adjusting the plot size per m<sup>2</sup> area to allow comparison between greenhouse and field plots.

The genotypes were grouped into three drought tolerance levels based on the grain yield obtained under drought-stressed conditions (Table 2.1). Genotypes with grain yield > 500 g m<sup>-2</sup> were considered drought tolerant, 300 to 500 g m<sup>-2</sup> as intermediate tolerant and < 300 g m<sup>-2</sup> as susceptible.

Table 1.1. Population groups based on observed drought tolerance levels of individual genotypes based on grain yield under drought-stress

<b>Tolerance level</b>	<b>Entry</b>						
<b>Tolerant</b>	BW100	BW111	BW116	BW120	BW147	BW149	BW151
	BW152	BW48	BW63	LM100	LM16	LM17	LM26
	LM29	LM37	LM51	LM71	LM76	LM90	
<b>Intermediate tolerant</b>	BW103	BW124	BW127	BW129	BW141	BW148	BW157
	BW159	BW162	BW49	BW58	BW71	BW80	LM01
	LM12	LM14	LM18	LM19	LM21	LM22	LM25
	LM27	LM30	LM31	LM32	LM36	LM39	LM40
	LM41	LM42	LM44	LM46	LM47	LM49	LM56
	LM58	LM60	LM70	LM72	LM79	LM83	LM85
	LM91	LM93	LM97	LM99			
<b>Susceptible</b>	BW128	BW140	BW142	BW145	BW150	BW28	LM15
	LM20	LM23	LM24	LM28	LM33	LM35	LM38
	LM43	LM48	LM50	LM52	LM54	LM55	LM57
	LM59	LM75	LM77	LM80	LM81	LM82	LM84
	LM86	LM96	LM98				

### 2.2.3 Analysis of phenotypic data

Data collected from each trial were subjected to Bartlett’s homogeneity of variance test prior to a combined analysis of variance (ANOVA) using the lattice procedure. Three-way interactions were assessed involving genotype, water regime and site in Genstat 18th edition (Payne et al., 2017). Data were subjected to significance tests using the Fischer’s Unprotected Least Significant Difference (LSD) at 5% probability. The adjusted means were further subjected to principal component analysis using SPSS version 25.0 software (IBM Corp. 2017) to assess genotype relatedness. Best linear unbiased predictors (BLUP) were calculated using the nlme package in R software (Pinheiro et al., 2013) across the environments to eliminate the environmental influence in downstream analysis. Hierarchical clusters were generated using phenotypic data based on the Gower method (Gower 1971). The phenotypic clusters were constructed using the Cluster package in R software (Maechler et al., 2013). Different phenotypic clusters were generated for the drought-stressed and non-stressed conditions.

### **2.2.4 Genotyping**

For DNA extraction, the 97 wheat genotypes were planted in seedling trays and raised in the greenhouse at UKZN. Genomic DNA was extracted using the modified CTAB method (Huang et al., 2000) from fresh leaves of three-week-old seedlings using Quick-DNA Microprep Plus (Zymo Research, Irvine, CA, USA) according to the manufacturer's procedures. Nucleic acid concentration and purity of the DNA were assessed using a NanoDrop 2000 spectrophotometer (ND-2000 V3.5, NanoDrop Technologies, Inc., Wilmington, DE, USA). The DNA samples were then sent to Diversity Arrays Technology (DArT) Pty Ltd. (Bruce, Australia) for genotyping by sequencing on the DArT platform.

### **2.2.5 Analysis of genotypic data**

The marker data were subjected to quality control using minor allele frequency, missing data and heterozygosity parameters. Markers with less than 5% minor allele frequency and more than 20% missing data were eliminated from the data. After that, 16,382 markers distributed across the 21 chromosomes were used in the final data analysis. Genotypes with more than 95% heterozygosity were eliminated from the analysis. Genetic parameters such as genetic distance (GD), polymorphism information content (PIC), minor allele frequency (MAF), observed heterozygosity ( $H_o$ ) and inbreeding coefficient (F) were calculated for the markers and individuals using the different population groups based on drought tolerance levels of individual genotypes (Table 2.1) using Powermarker V3.25 software (Liu and Muse, 2005). Hierarchical clusters were generated using genotypic data based on Jaccard's coefficient (Jaccard 1908). A joint hierarchical cluster was generated using combined data from genotypic and phenotypic dissimilarity matrices. The clusters were constructed using the "Cluster" package in R software (Maechler et al., 2013). Analysis of molecular variance was conducted using the different population groups based on drought tolerance levels (Table 2.1) using Powermarker V3.25. The genotype hierarchical cluster was compared to the drought-stressed and non-stressed hierarchical cluster using the "Viridis" package in R (Garnier et al., 2018) to observe grouping patterns between genotypic and phenotypic data.

## **2.3 Results**

### **2.3.1 Phenotyping**

#### **2.3.1.1 Genotype and water regime effects on agronomic traits and grain yield**

The recorded traits including PB, SB, RB, RS and GY, exhibited significant genotypic and site variability, while the water regime was significant for all assessed traits except DTH. The effects of the three-way interaction involving genotype, site and water regime were significant for DTM, TN and RS (Table 2.2). The genotype  $\times$  site interaction had a significant impact on all traits apart from GY. On the other hand, the DTH and DTM response was significantly affected by the interaction between genotypes and water regimes.

Genotypes LM52 (with grain yield of  $929.40 \text{ g m}^{-2}$ ), LM30 ( $927.70 \text{ g m}^{-2}$ ) and BW157 ( $782.00 \text{ gm}^{-2}$ ) were the highest yielding genotypes with high root biomass ( $> 200 \text{ gm}^{-2}$ ) under drought stress. The phenotypic data showed wide ranges between the minimum and maximum values for each of the traits. GY and RB had ranges of  $731.40 \text{ g m}^{-2}$  and  $400 \text{ g m}^{-2}$ , respectively, under drought-stressed conditions (Table 2.3). Higher variability was observed under non-stressed conditions than drought-stressed for TN, PB, SB and GY and vice-versa for DTH, DTM, PH, RB and RS as observed among the range of values.

Table 2.2. Mean square values and significant tests after combined analysis of variance of biomass and yield-related traits of 97 wheat genotypes evaluated under non-stressed and drought-stressed conditions

SOV	df	DTH	DTM	PH	TN	PB	SB	RB	RS	GY
<b>Block</b>	19	96.00***	225.91***	999.83***	18.00***	7029511.00***	2506321.00***	66525.00***	0.03*	876453.00***
<b>Rep</b>	1	261.72***	552.71***	7673.14***	68.44***	31575567.00***	15118430.00***	157718.00***	0.01	2285866.00***
<b>Genotype (Gen)</b>	96	197.51***	124.22***	167.49***	16.05***	711194.00*	270175.00***	15507.00***	0.03*	146304.00*
<b>Water Regime (WR)</b>	1	53.60	28022.20***	31765.90***	3358.07***	110774907.00***	22763489.00***	1883093.00***	1.11***	18109833.00***
<b>Site</b>	2	74612.12***	125380.64***	134122.84***	2746.88***	1594700477.00***	617123646.00***	11896156.00***	35.55***	192151512.00***
<b>Gen*WR</b>	96	22.31*	39.93***	30.77	5.07	437549.00	144938.00	11995.00	0.02	82041.00
<b>Gen*Site</b>	192	85.02***	61.80***	65.12***	9.69***	657583.00*	267142.00***	15107.00***	0.02**	123754.00
<b>Gen*WR*Site</b>	192	19.72	35.19***	35.91	7.42**	495229.00	156342.00	11818.00	0.03*	92026.00
<b>Residual</b>	561	17.21	23.47	30.18	5.43	532134.00	160226.00	10445.00	0.02	106404.00

SOV = source of variation, df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, PB = total plant biomass (g m<sup>-2</sup>), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), RS = root to shoot ratio GY = grain yield (g m<sup>-2</sup>), Rep = replication, Gen = genotype, WR = water regime

Table 2.3. Mean values of the 10 best genotypes and five bottom genotypes based on grain yield (GY) under drought-stress for nine agronomic traits of 97 bread wheat lines under drought-stressed (DS) and non-stressed (NS) conditions

ENTRY	DTH		DTM		PH		TN		PB		SB		RB		RS		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
<b>Top ten genotypes</b>																		
<b>LM52</b>	56.51	64.52	103.80	118.10	60.60	75.94	9.83	15.84	2137.00	3089.00	994.00	1487.00	214.20	352.40	0.43	0.53	929.40	1249.90
<b>LM30</b>	66.12	66.73	109.30	116.30	67.12	82.39	11.11	12.13	2513.00	2600.00	1260.00	1370.00	325.90	295.40	0.50	0.49	927.70	934.40
<b>BW157</b>	65.13	65.85	104.40	114.80	65.42	75.11	7.94	10.84	2091.00	2145.00	1060.00	1042.00	249.40	298.10	0.42	0.53	782.00	802.60
<b>BW152</b>	64.39	65.53	108.60	116.80	65.09	75.73	10.36	11.50	1672.00	2417.00	945.00	1266.00	218.30	453.10	0.49	0.60	509.10	699.50
<b>BW140</b>	68.16	57.36	108.50	115.60	69.72	66.36	7.59	15.85	1559.00	1978.00	850.00	1168.00	228.40	310.00	0.46	0.49	481.70	497.30
<b>LM47</b>	69.05	67.27	112.00	121.10	65.35	78.57	9.10	12.25	1460.00	2901.00	898.00	1661.00	171.20	311.70	0.39	0.61	469.00	926.70
<b>LM70</b>	68.25	68.83	109.20	119.00	68.11	74.79	8.61	13.84	1478.00	1990.00	839.00	990.00	190.90	274.90	0.48	0.57	449.10	722.10
<b>LM48</b>	71.99	65.67	112.30	118.50	63.74	83.69	9.01	10.00	1606.00	2335.00	921.00	1181.00	238.40	276.80	0.40	0.55	447.40	876.70
<b>BW162</b>	63.85	63.65	108.80	114.80	66.69	78.79	8.79	12.35	1358.00	2639.00	788.00	1288.00	160.70	280.00	0.45	0.62	414.70	1068.40
<b>LM54</b>	61.50	69.71	105.80	119.70	60.62	78.49	11.00	11.67	1157.00	2952.00	653.00	1739.00	136.20	424.50	0.44	0.57	368.00	789.40
<b>Bottom five genotypes</b>																		
<b>LM39</b>	69.16	68.61	109.00	118.50	66.39	79.89	7.68	13.03	1290.00	2195.00	799.00	1147.00	208.90	305.30	0.42	0.52	281.50	741.30
<b>LM44</b>	70.22	66.17	102.60	113.00	66.61	83.28	9.20	12.84	1186.00	2174.00	716.00	1286.00	189.60	213.80	0.49	0.39	281.50	674.10
<b>BW147</b>	73.45	67.16	111.00	117.40	65.07	76.27	7.34	9.70	1441.00	2167.00	940.00	1140.00	218.50	346.00	0.43	0.52	278.90	680.70
<b>LM55</b>	65.43	63.15	108.10	113.70	60.29	76.94	9.00	14.45	1127.00	2034.00	778.00	1133.00	131.90	210.50	0.32	0.39	216.30	679.80
<b>LM29</b>	64.83	66.39	112.80	122.90	62.22	80.86	8.50	13.08	1062.00	2662.00	710.00	1694.00	186.50	272.20	0.40	0.48	198.00	870.20
<b>Mean</b>	65.64	65.90	107.40	117.70	65.32	78.67	9.22	12.75	1490.00	2298.00	853.50	1252.00	206.20	295.10	0.43	0.49	444.30	757.10
<b>SEM</b>	0.85	0.41	0.47	0.30	0.49	0.44	0.10	0.16	23.86	37.75	13.26	24.68	4.87	6.05	0.01	0.01	12.19	15.48
<b>CV (%)</b>	12.72	6.16	4.33	2.49	7.35	5.52	10.81	12.63	15.77	16.18	15.31	19.42	23.26	20.19	13.99	13.04	26.88	20.14
<b>Range</b>	28.19	21.45	26.10	16.70	42.73	19.84	5.22	7.74	1451.00	2257.00	767.00	1498.00	400.00	268.50	0.34	0.30	731.40	825.60
<b>LSD (5%)</b>	4.30	5.29	6.61	4.17	6.68	4.87	0.35	3.16	532.70	1053.00	274.80	591.30	74.81	148.6	0.13	0.16	274.20	449.20
<b>R<sup>2</sup> (%)</b>	80.86	72.25	77.06	82.45	76.48	74.24	44.81	33.04	79.70	76.79	78.78	73.41	14.99	20.71	19.43	42.68	62.26	68.91

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, PB = total plant biomass (g m<sup>-2</sup>), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), RS = root to shoot ratio GY = grain yield (g m<sup>-2</sup>), DS = drought-stressed, NS = non-stressed, SEM = standard error of mean, CV = coefficient of variation, LSD = least significant difference, R<sup>2</sup> = coefficient of determination

### **2.3.1.2 Principal components of phenotypic data**

The first three components with Eigenvalues above 1.00 accounted for 70.86% of the total variation under drought-stressed conditions (Table 2.4). Total plant biomass (0.92), shoot biomass (0.87), root biomass (0.73) and grain yield (0.74) had the highest contributions to the variation explained by the first principal component (PC1), which accounted for 33.92% of the total variation. The second principal component (PC2) explained 21.87% of the total variation and was associated with the DTH (0.83) and DTM (0.74), which had the highest contributions to this principal component. Root-to-shoot ratio (0.87) had the highest contribution to the third principal component (PC3), which accounted for 15.08% of the total variation.

Under non-stressed conditions, the first three PCs with Eigenvalues above 1.00 explained 68.60% of the total variation among the genotypes (Table 2.4). Notably, PB (0.97), SB (0.86), RB (0.70) and GY (0.75) had the highest contributions to PC1, which explained 31.80% of the total variation. The highest loadings on PC2 were contributed to by DTH (0.88) and DTM (0.74). Plant height (0.71) had the highest loading on PC3, which accounted for 14.81% of the variation. Root-to-shoot ratio and RB had negative loadings of  $-0.74$  and  $-0.44$ , respectively, on PC3.

Table 2.4. Principal component scores and variance of traits measured on 97 wheat genotypes assessed under drought-stress and non-stress conditions

Traits	Drought-stressed			Non-stressed		
	PC1	PC2	PC3	PC1	PC2	PC3
<b>DTH</b>	0.35	0.83	0.05	0.14	0.88	0.10
<b>DTM</b>	0.40	0.74	-0.08	0.19	0.74	0.01
<b>PH</b>	0.13	0.13	-0.46	0.14	0.39	0.71
<b>TN</b>	-0.12	-0.56	-0.15	-0.05	-0.53	0.10
<b>PB</b>	0.94	-0.29	-0.15	0.97	-0.17	0.12
<b>SB</b>	0.87	-0.03	-0.27	0.86	-0.07	0.22
<b>RB</b>	0.73	0.08	0.50	0.70	0.10	-0.44
<b>RS</b>	0.18	-0.19	0.87	0.22	0.29	-0.74
<b>GY</b>	0.74	-0.53	-0.12	0.75	-0.33	0.08
<b>Eigenvalue</b>	3.05	1.97	1.36	2.86	1.98	1.33
<b>Explained variance (%)</b>	33.92	21.87	15.08	31.80	21.99	14.81
<b>Cumulative variance (%)</b>	33.92	55.79	70.86	31.80	53.79	68.60

PC = principal component, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, PB = total plant biomass ( $\text{g m}^{-2}$ ), SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), RS = root to shoot ratio and GY = grain yield ( $\text{g m}^{-2}$ )

### 2.3.1.3 Phenotypic hierarchical clustering

Using phenotypic data, hierarchical cluster analysis allocated the wheat genotypes into three groups under non-stressed conditions (Figure 2.1). The largest cluster (cluster II) contained 45 genotypes, followed by the second largest cluster (cluster III) with 37 genotypes. In general, cluster II contained late maturing genotypes with low plant biomass and grain yield. High yielding genotypes (LM52, BW63 and BW127) were grouped in cluster I, which was characterized by shorter genotypes with early heading, high RB (BW148 and BW152) and high tiller number. Cluster III consisted of genotypes with high root biomass and late flowering.

The genotypes were also grouped into three groups under drought-stress conditions (Figure 2.2). The first and second largest clusters (cluster III and cluster II, respectively) had 62 and 23 genotypes, respectively, while cluster I had 12 genotypes only. Cluster III consisted of late heading and maturity genotypes with high root-to-shoot ratios. Genotypes with early maturity and low plant biomass were grouped in cluster I. Cluster II contained genotypes with high root and plant biomass and early heading. However, there were some high-yielding genotypes in each cluster.

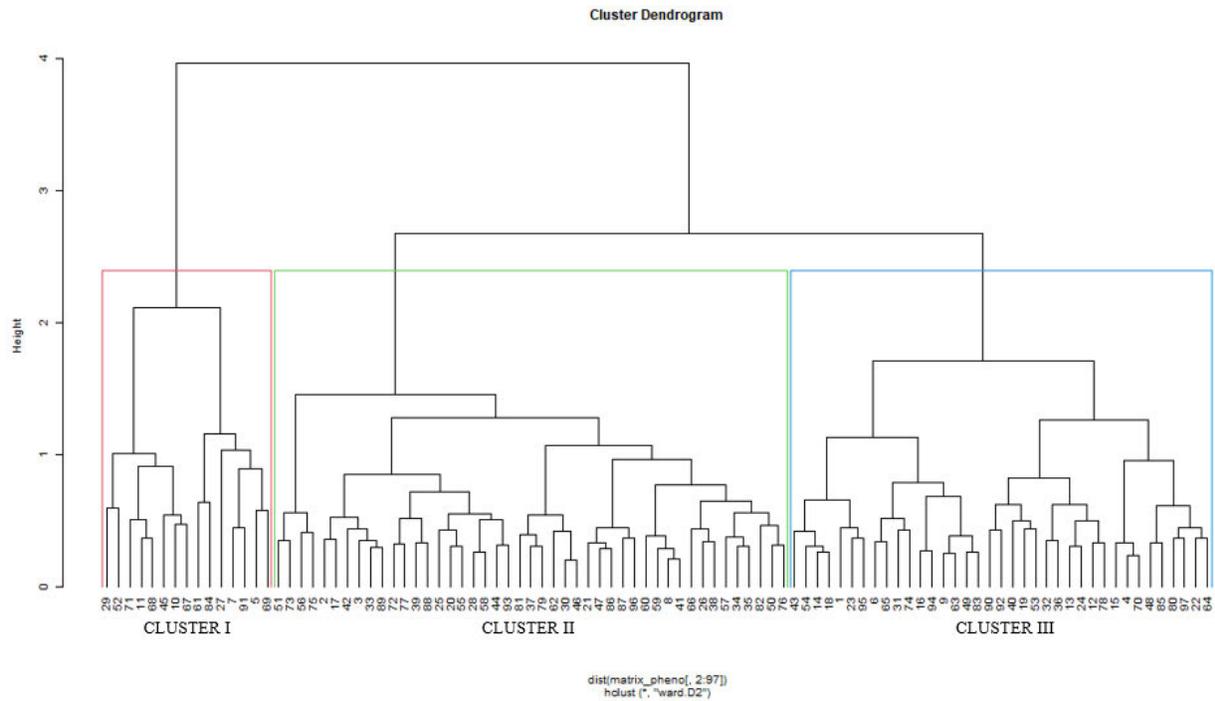


Figure 2.1. Hierarchical clustering of 97 wheat genotypes based on phenotypic traits measured under non-stressed conditions. Clusters are separated by colour lines.

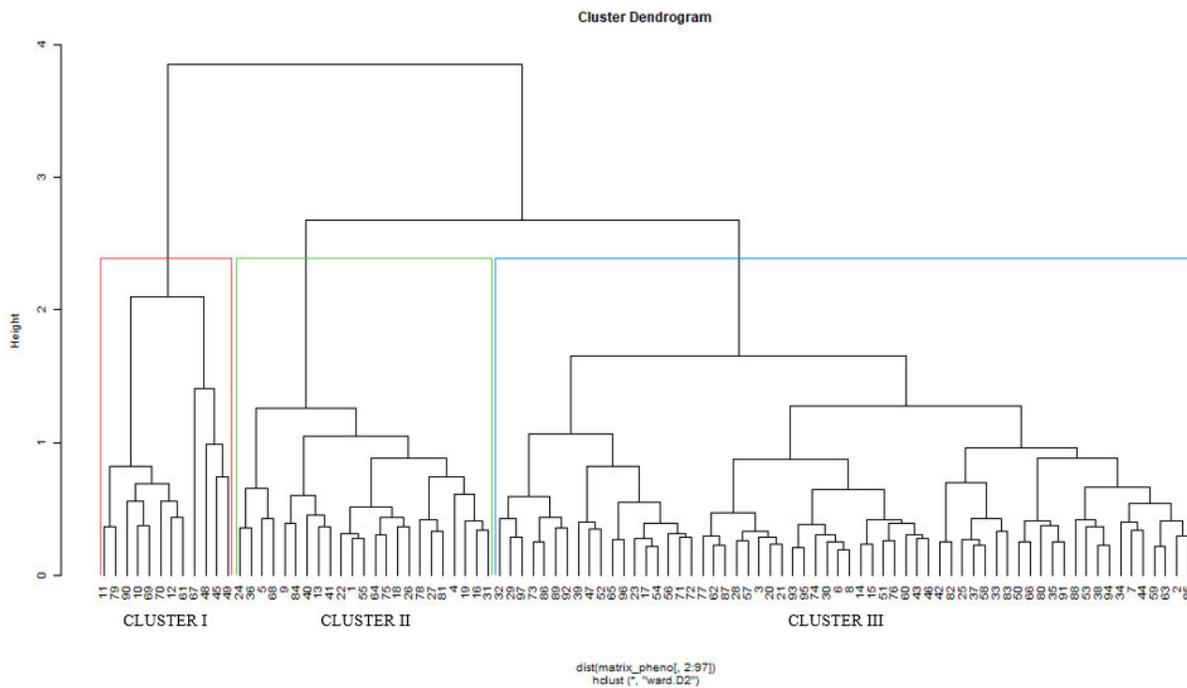


Figure 2.2. Hierarchical clustering of 97 wheat genotypes based on phenotypic traits measured under drought-stressed conditions. Clusters are separated by colour lines.

## 2.3.2 Genotyping

### 2.3.2.1 Population genetic parameters based on SNP markers

The general pattern showed that the average values of the genetic parameters did not vary widely among the different populations of highly drought-tolerant, intermediate tolerant and susceptible genotypes (Table 2.5). The genetic distances of the different populations ranged from 0.20 to 0.88. The polymorphic information content showed that the tested markers contained non-polymorphic and highly polymorphic markers. The lowest PIC was 0.24, while the highest was 1. The average minor allele frequency was highest for the susceptible genotypes (0.47) and was lowest for drought-tolerant genotypes (0.43). The genotypes exhibited high levels of heterozygosity, ranging between 0.29 and 0.58. The in-breeding coefficient had lower and upper values of  $-0.60$  and  $0$ , respectively.

Table 2.5. Genetic parameters of 97 wheat genotypes genotyped with 16 382 SNP markers

Population	GD	PIC	MAF	Ho	F
<b>Drought tolerant</b>	0.63	0.75	0.38	0.43	-0.38
<b>Intermediate tolerance</b>	0.64	0.80	0.44	0.39	-0.33
<b>Susceptible</b>	0.63	0.81	0.47	0.38	-0.32
<b>Range</b>	0.20 - 0.88	0.24 – 1.00	0.05 - 0.50	0.29 - 0.58	0 - -0.60

GD = genetic distance, PIC = polymorphic information content, MAF = minor allele frequency, Ho = observed heterozygosity, and F = inbreeding coefficient

### 2.3.2.2 Analysis of molecular variance and genotypic hierarchical clustering

Analysis of molecular variance was conducted based on observed drought tolerance levels of individual genotypes using phenotypic data (Table 2.6). The within-population variation was very high (99%) with a negligible among-population variation of 1% (Table 2.6).

Table 2.6. Analysis of molecular variance among 97 wheat genotypes genotyped with 16 382 SNP markers

Source	df	SS	MS	Estimated Variance	Proportion of variance
Among Pops	2	7713.672	3856.836	21.935	1%
Within Pops	94	299495.668	3186.124	3186.124	99%
Total	96	307209.340		3208.059	100%

df = degrees of freedom, SS = sum of squares, MS = mean squares, and Pops = Populations

The genotypes were grouped into three heterogeneous clusters based on the SNP markers (Figure 2.3). The largest cluster (cluster III) had 46 genotypes, followed by cluster I with 30 and cluster II with 21. Cluster III contained genotypes from the International Bread Wheat Screening Nursery (IBWSN) program at CIMMYT and three from the 6th Heat Tolerant Wheat Screening Nursery (HTWSN) designated as LM23, LM47 and LM48. Common parents for most genotypes in this cluster included 0B, WGY and 099TOPY. Cluster I and Cluster II consisted of genotypes that were part of the HTWSN.

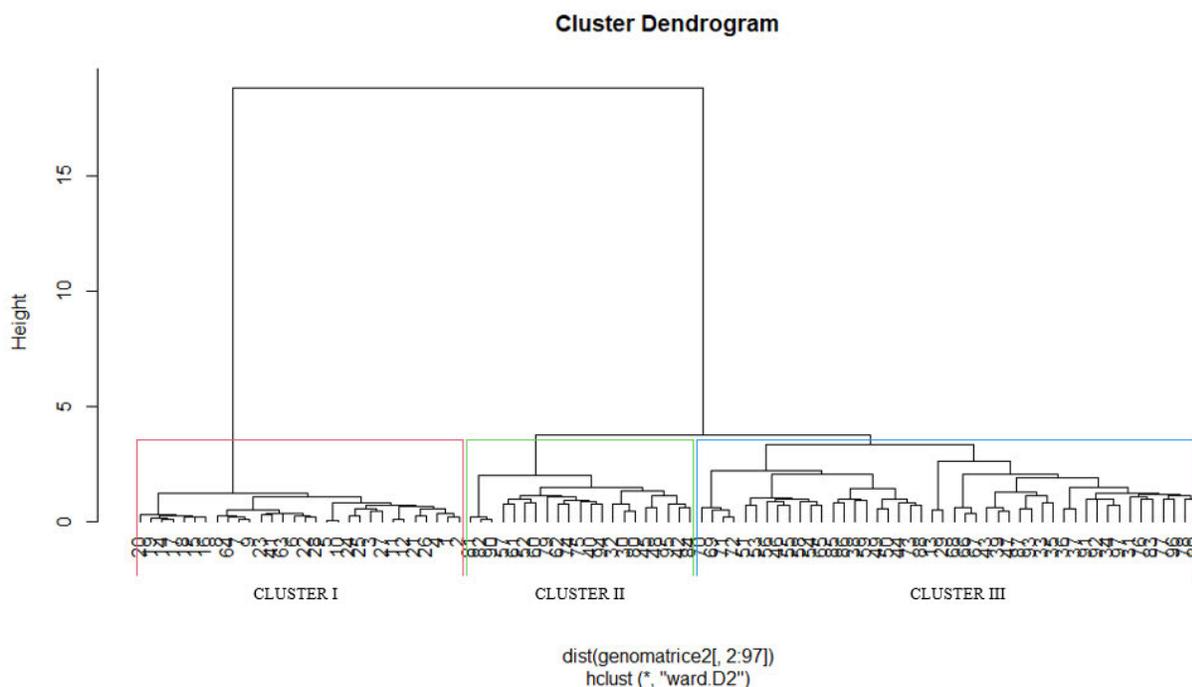


Figure 2.3. Hierarchical clustering of 97 wheat genotypes based on 16 382 SNP markers. Clusters are separated by colour lines.

### 2.3.3 Comparison of phenotypic and genotypic hierarchical clusters

A comparison of genetic and phenotypic clusters was conducted to determine genotype consistency between different dendrograms. None of the genotypes maintained their positions when genotypic hierarchical clusters were compared to phenotypic clustering under non-stress conditions (Figure 2.4). Similarly, the genotypic clustering was discordant with the phenotypic clusters under drought-stressed conditions (Figure 2.5). Under drought stress, only two genotypes (LM56 and LM57) maintained their positions across the genotypic and phenotypic dendrograms. The tanglegram comparison showed that 44% of the genotypes under drought stress maintained their cluster membership in the genotypic and phenotypic hierarchical clustering (Figure 2.4).

Under non-stress conditions, only 28% of genotypes maintained their membership in the genotypic and phenotypic hierarchical clustering (Figure 2.5). Three different clusters were revealed by the joint matrix of pheno-typic and genotypic data (Figure 2.6).

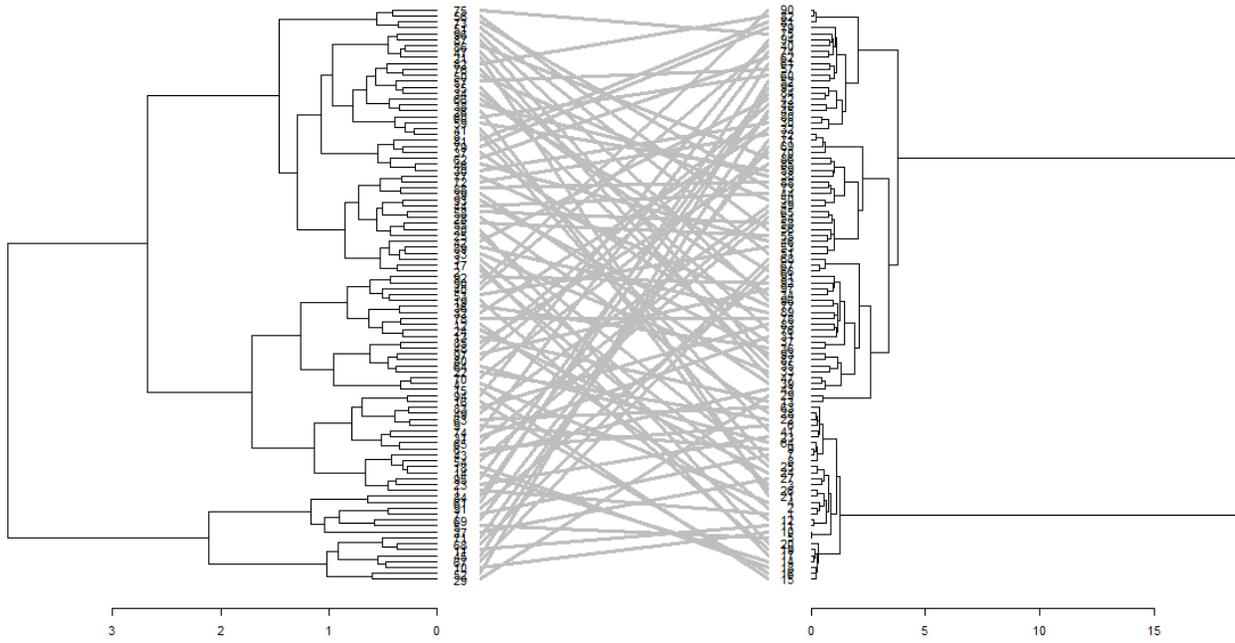


Figure 2.4. Tanglegram comparison of genotypic and phenotypic hierarchical clusters of 97 wheat genotypes based on 16 382 SNP markers and phenotypic data measured under non-stressed conditions

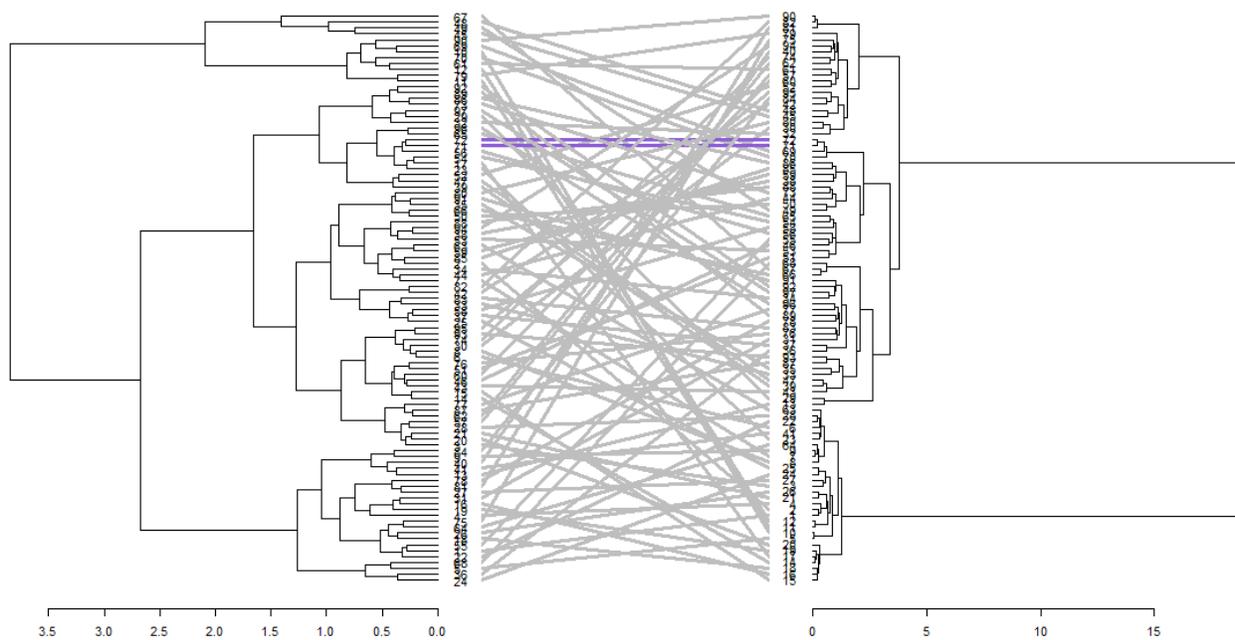


Figure 2.5. Tanglegram comparison of genotypic and phenotypic hierarchical clusters of 97 wheat genotypes based on 16 382 SNP markers and phenotypic data measured under drought-stressed conditions

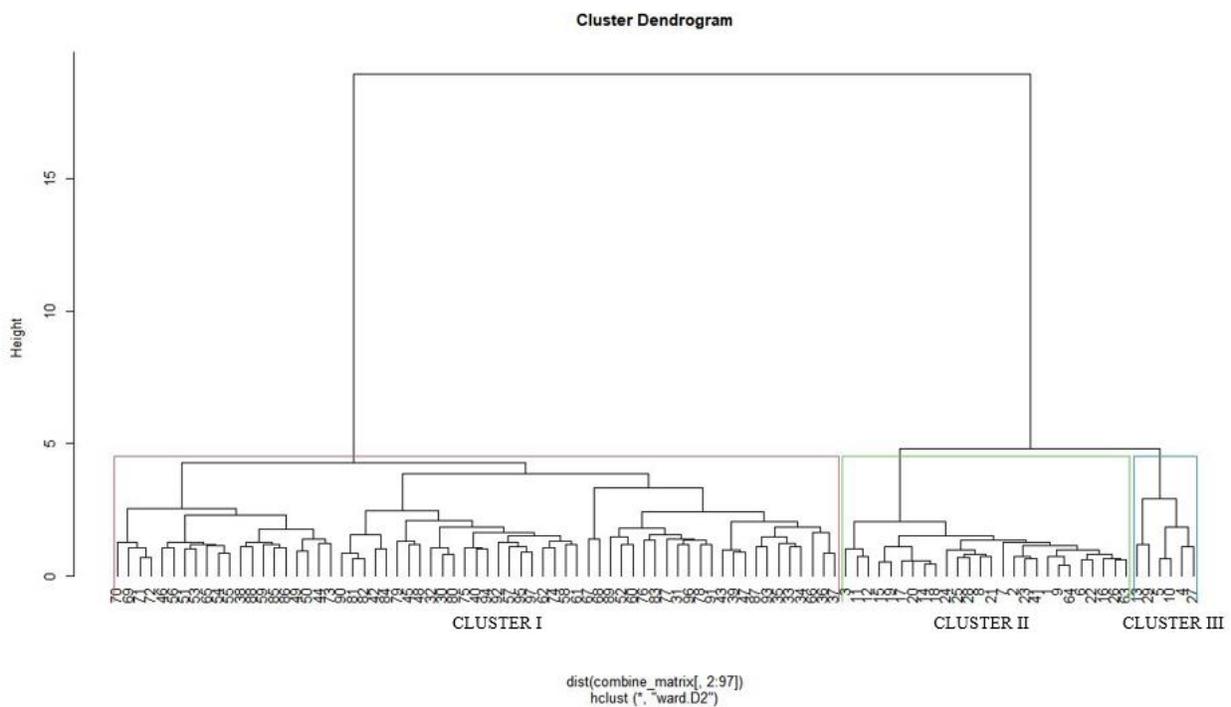


Figure 2.6. Joint hierarchical clustering of 97 wheat genotypes based on phenotypic data and 16 382 SNP markers. Clusters are separated by colour lines.

## **2.4 Discussion**

### **2.4.1 Genotypic variation for agronomic traits and biomass allocation**

The effect of crop genetics, water availability and growth site on biomass partitioning was strong. Different genotypic responses for key traits (Table 2.2) such as plant biomass, shoot biomass, root biomass, root-to-shoot ratio and grain yield in the same environments reflect a high genotype by environment interaction and presence of genetic diversity for these traits (Nehe et al., 2019). Substantial differences in the allocation of biomass and carbon between roots and shoots of different cultivars have been observed with influence from biomass-related traits such as tillering ability (Hendriks et al., 2016) and plant height (Bai et al., 2013). Manipulating these traits to optimize biomass allocation to roots would increase the capacity of crops to support higher biomass production and grain yield in the absence of sufficient soil moisture (He et al., 2011). Schneider and Lynch (2020) propose the use of root plasticity as a target trait in plant breeding programs to stabilize crop productivity across diverse environments. Thus, a better understanding of the contribution of roots to yield is important in breeding climate-smart crops. Hence, plant breeders will need to integrate root phenotyping to improve wheat productivity in resource-poor wheat production environments (Waines and Ehdaie 2007).

### **2.4.2 Multivariate relationships explained by principal components**

The presence of high genetic variation in this panel of genotypes can be exploited to develop breeding populations and identify recombinants with superior traits for drought adaptation. The high contributions of plant biomass, shoot biomass, root biomass and grain yield on the first principal component indicate that these traits were the most important in explaining the variation among the genotypes (Table 2.4). Passioura (1983) and Palta et al., (2011) suggest that optimizing biomass allocation will provide more benefits in selection as opposed to increasing one parameter of biomass such as root biomass alone. These traits can therefore be used together for parental selection to develop breeding populations with improved biomass allocation for both grain yield and root biomass as observed by Bektas et al., (2016). This will increase the adaptability of wheat cultivars across a diverse range of environments, as the traits indicated above were important in explaining variation under both drought-stressed and non-stressed conditions.

### **2.4.3 Phenotypic clustering of genotypes and implications for drought tolerance and carbon sequestration breeding**

Genotypes such as LM52, BW63 and BW127 that were grouped in cluster I under non-stressed conditions (Figure 2.1) can be selected to develop breeding populations for improving grain yield in wheat. This cluster also contained generally short genotypes with early heading and high root biomass, which are critical attributes for drought escape and carbon sequestration potential. Early heading has been exploited in crop improvement programs to develop cultivars that can complete their growth cycle before the onset of terminal drought stress (Gao et al., 2018). High root biomass exhibited by the genotypes in this cluster will be useful for improving root systems in wheat. Extensive rooting ability renders an advantage in moisture-stressed conditions by increasing crop access to water in deeper soil profiles (Sinclair 2011) while also contributing to nutrient recycling, especially carbon by rhizo-deposition (Hirte et al., 2018). Breeding for shorter plants with improved harvest indices and lodging resistance was exploited in the green revolution with great success (Du et al., 2018). On the other hand, tall plants usually have higher biomass than shorter plants which contributes to carbon sequestration; however, tall plants are prone to lodging, which negatively impacts grain yield (Shamuyarira et al., 2019). Genotypes from cluster III under drought-stress (Figure 2.2) were generally late maturing, making them ideal for long-season environments that are not prone to terminal droughts (Figueroa-Bustos et al., 2019). In the optimal production conditions, it would be ideal to cultivate late maturity genotypes to maximize irradiation and moisture availability because early maturing genotypes incur a yield penalty due to accelerated growth and development (Aslam et al., 2017). For carbon sequestration, late maturity genotypes have prolonged periods for carbon assimilation in the biosphere. However, under drought conditions, these positive attributes increase the susceptibility of these genotypes to moisture stress. The high root-to-shoot ratios observed in cluster III would be useful during breeding for optimised biomass allocation (Mathew et al., 2019). High root-to-shoot ratios indicate that the root systems of these genotypes were large enough to support the above-ground structures and possibly provided a means for increased carbon deposition in the soil (Hu et al., 2018).

### **2.4.4 Genotypic clustering and molecular variance**

The low variability of the genetic parameters among the populations indicates a narrow genetic base, which could be from common parentage; the genotypes were mainly sourced from CIMMYT's heat and drought stress nurseries. A considerable number of genotypes had one or two

common parents in their pedigrees. The use of a select few elite parents is common in modern breeding programs. This has led to a focus on improving target traits and discarding any material that does not meet the breeding objectives (van Ginkel and Ogonnaya 2007). However, the continuous use of a few selected lines contributes to narrowing genetic diversity for important traits such as rooting ability, which predisposes modern cultivars to moisture and nutrient deficiencies (Fu 2015; Girma 2017). Landraces possess genetic variation for drought adaptive traits, which are absent in modern cultivars and can be harnessed in breeding programs to develop new cultivars with enhanced stress tolerance (Naderi et al., 2020). The major challenge would be the need to break linkage with unfavorable traits often encountered when using landraces.

The unexpectedly high level of heterozygosity observed in the population (Table 2.5) could provide an opportunity to develop new segregants for wheat improvement. Ideally, the population was expected to exhibit lower levels of heterozygosity because the genotypes were advanced generations. However, high levels of heterozygosity have also been observed in advanced wheat lines (Bhatta et al., 2018), providing a basis for developing new and useful recombinants after mating divergent genotypes. It would be imperative to select the most genetically distant and phenotypically divergent genotypes for developing breeding populations and crosses that may be advanced for release as varieties.

Cluster analysis grouped genotypes from drought and heat tolerant nurseries in the same clusters indicating that these genotypes are closely related. Heat and drought tolerance are highly correlated, and common genomic loci coding for the combined effect of heat and drought stresses have been identified (Havaux et al., 1988; Rampino et al., 2012; Acuña-Galindo et al., 2015). Drought-adaptive secondary traits such as stay-green characteristics and delayed senescence are also observed in wheat genotypes that are tolerant to heat stress indicating that common physiological processes may be responsible for plant response to both drought and heat stress (Tricker et al., 2018).

The molecular variance analysis (Table 2.6) showed that the intrapopulation variance was very high at 99%, with minimal inter-population variance (1%). Autogamous crops like wheat are characterized by low cross-fertilization. This will suppress deleterious genes and promote high intrapopulation diversity observed within the populations (Ennos, 1983; Dreisigacker et al., 2005). This high variation can be exploited to develop new breeding populations with higher productivity

than the parental genotypes. The low among-population variance among the populations indicates that similar genetic gains could be achieved even by selecting divergent genotypes within the same populations.

#### **2.4.5 Genotypic and phenotypic divergence under different water regimes**

Genetic markers reveal allelic diversity, while phenotypic traits are important indicators of genotype performance in a given environment. As such, the genotype and phenotypic clusters under both water conditions were largely inconsistent because of genotype–environment interactions, which caused fluctuations of phenotypic expression in morphological traits (Royo et al., 2010). The inconsistent genetic and phenotypic clustering under both soil moisture conditions can also be attributed to low precision in phenotyping some traits (Haghighattalab et al., 2016), especially root traits that are subject to large environmental variance. Despite the differences constantly observed between genotype and phenotype clusters, the methods are complementary and are useful in assessing wheat genetic diversity for drought tolerance and carbon sequestration as they provide a foundation for identifying underlying genetic control of these traits. Thus, the complementary use of genetic and phenotypic markers in selection would improve selection efficiency by consolidating all the variation in the individuals (Agre et al., 2019).

Higher consistency in the genotypic and phenotypic clustering under drought-stressed conditions compared to non-stressed conditions could be due to the selection pressure exerted by the drought treatment. Drought induces drought-adaptive biochemical and physiological processes that differ in intensity and duration, resulting in variable phenotypic expression among cultivars (Saint Pierre et al., 2012; Ahmed et al., 2020). In addition, certain genes that confer drought tolerance are only induced in response to stress and dehydration in the plant (Saint Pierre et al., 2012). In the absence of stress, these genetic regions will not be activated, and thus, it will not be ideal for identifying quantitative trait loci or superior lines in a panel of genotypes with similar underlying responses to soil moisture dynamics. Therefore, multi-environment trials would provide more information on genotype performance by considering different selection pressures exerted by the environments, thereby increasing consistency in the grouping of genotypes.

The joint matrix of phenotypic and genotypic data was used to consolidate the genotypic and phenotypic data to group the genotypes into different heterotic groups to select genotypes for combining ability analysis. This provides the opportunity to select based on both phenotypic and

molecular data. Genotypes LM30, LM48, LM52, LM54 and LM70, were selected from cluster I and BW152, BW157, BW162 and LM47 were selected from cluster II. One genotype (BW140) was selected from cluster III, which consisted of only six genotypes. The selected genotypes were divergent and had high grain yield and root bio-mass.

## 2.5 Conclusions

The study revealed the presence of genetic variation that is useful for developing climate-smart and drought-adapted wheat varieties. Principal component analysis revealed that PB, SB, RB and GY explained most of the variation among the genotypes under drought-stressed and non-stressed conditions. Genetic parameters varied widely with the genetic distance, polymorphic information content and expected heterozygosity ranges of 0.20–0.88, 0.24–1.00 and 0.29–0.58, respectively. Analysis using genotypic and phenotypic data resolved three heterotic groups and allowed for the selection of desirable parents for combining ability analysis. Information gathered in this study was important in highlighting the utility of biomass allocation partitioning and how it can be utilised to develop new breeding populations to produce climate-smart cultivars more adaptable to changing edaphic and climatic conditions. We recommend conducting genetic diversity analysis in more environments under more stress intensity to capture the variation due to the genotype–environment interaction, and ascertain the consistency of the information gathered from phenotypic and molecular data. Our data suggest that landraces, older varieties, and obsolete cultivars should be included to broaden the genetic diversity for biomass allocation and yield-related traits. Moreover, we propose the use of additional drought tolerance indices as indicators of drought tolerance to complement yield measurements under stress.

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Appendix 2.1. Names of genotypes and their respective pedigrees used in this study

ENTRY	PEDIGREE
	Genotypes from CIMMYT Heat Stress Tolerance Nursery
<b>BW28</b>	CMSA05Y01011T-040M-040ZTP0Y-040ZTM-040SY-14ZTM-03Y-0B
<b>BW48</b>	CMSA04M00346S-040ZTP0Y-040ZTM-040SY-27ZTM-04Y-0B
<b>BW49</b>	CMSA04M00346S-040ZTP0Y-040ZTM-040SY-28ZTM-01Y-0B
<b>BW58</b>	CMSA04M00067S-040ZTB-040ZTY-040ZTM-040SY-2ZTM-02Y-0B
<b>BW63</b>	CMSA04M01020T-050Y-040ZTP0M-040ZTY-040ZTM-040SY-5ZTM-03Y-0B
<b>BW71</b>	CMSA05Y00325S-040ZTP0Y-040ZTM-040SY-7ZTM-01Y-0B
<b>BW103</b>	CMSS05B00581S-099Y-099M-099Y-099ZTM-2WGY-0B
<b>BW111</b>	CMSS05B00663S-099Y-099M-099Y-099ZTM-13WGY-0B
<b>BW116</b>	CMSS05B00742S-099Y-099M-099Y-099ZTM-5WGY-0B
<b>BW124</b>	CGSS05B00153T-099TOPY-099M-099NJ-22WGY-0B
<b>BW127</b>	CGSS05B00162T-099TOPY-099M-099Y-099ZTM-15WGY-0B
<b>BW128</b>	CGSS05B00162T-099TOPY-099M-099NJ-13WGY-0B
<b>BW129</b>	CGSS05B00162T-099TOPY-099M-099NJ-099NJ-7WGY-0B
<b>BW141</b>	CGSS05B00243T-099TOPY-099M-099NJ-099NJ-1WGY-0B
<b>BW142</b>	CGSS05B00243T-099TOPY-099M-099NJ-099NJ-2WGY-0B
<b>BW145</b>	CGSS05B00253T-099TOPY-099M-099Y-099ZTM-8WGY-0B
<b>BW147</b>	CGSS05B00256T-099TOPY-099M-099NJ-099NJ-5WGY-0B
<b>BW148</b>	CGSS05B00258T-099TOPY-099M-099Y-099ZTM-3WGY-0B
<b>BW149</b>	CGSS05B00258T-099TOPY-099M-099Y-099ZTM-11WGY-0B
<b>BW150</b>	CGSS05B00258T-099TOPY-099M-099Y-099ZTM-12WGY-0B
<b>BW151</b>	CGSS05B00258T-099TOPY-099M-099Y-099ZTM-13WGY-0B
<b>BW152</b>	CGSS05B00258T-099TOPY-099M-099NJ-1WGY-0B
<b>BW157</b>	CGSS05B00261T-099TOPY-099M-099NJ-099NJ-8WGY-0B
<b>BW157</b>	CGSS05B00261T-099TOPY-099M-099NJ-099NJ-8WGY-0B
<b>BW159</b>	CGSS05B00290T-099TOPY-099M-099NJ-099NJ-7WGY-0B
<b>BW162</b>	CGSS05B00304T-099TOPY-099M-099NJ-099NJ-3WGY-0B
<b>LM01</b>	ACHTAR*3//KANZ/KS85-8-5/4/MILAN/KAUZ//PRINIA/3/BAV92/5/MILAN/KAUZ//PRINIA/3/BAV92
<b>LM12</b>	SOKOLL/ROLF07
<b>LM14</b>	MILAN/KAUZ//PRINIA/3/BAV92/4/WBLL1*2/KUKUNA
<b>LM15</b>	RL6043/4*NAC//PASTOR/3/BAV92/4/ATILIA/BAV92//PASTOR
<b>LM16</b>	PASTOR*2/BAV92/3/FRET2/KUKUNA//FRET2
<b>LM17</b>	ESDA/KKTS
<b>LM18</b>	GOUBARA-1/2*SOKOLL
<b>LM19</b>	SOKOLL*2/4/CHEN/AEGILOPS SQUARROSA (TAUS)//FCT/3/STAR
<b>LM20</b>	PBW343
<b>LM21</b>	PRL/2*PASTOR
<b>LM22</b>	MUNAL #1

## Appendix 2.1 continued

ENTRY	PEDIGREE
	Genotypes from CIMMYT Heat Stress Tolerance Nursery
LM23	QUAIU
LM24	WBLL1*2/BRAMBLING
LM25	WHEAR//2*PRL/2*PASTOR
LM26	ATTILA*2/PBW65//TAM200/TUI
LM27	YUNMAI 48//2*WBLL1*2/KURUKU
LM28	ATTILA/3*BCN//BAV92/3/TILHI/4/SHA7/VEE#5//ARIV92
LM29	PRL/2*PASTOR*2//SKAUZ/BAV92
LM30	C80.1/3*BATAVIA//2*WBLL1/3/ATTILA/3*BCN*2//BAV92/4/WBLL1*2/KURUKU
LM31	ATTILA*2/HUITES//FINSI/3/ATTILA*2/PBW65
LM32	ATTILA*2//CHIL/BUC*2/3/KUKUNA
LM33	ATTILA*2/PBW65//KACHU
LM35	WBLL1//UP2338*2/VIVITSI
LM36	WBLL1*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/KACHU
LM37	KACHU/SAUAL
LM38	SAUAL/3/MILAN/S87230//BAV92
LM39	ATTILA/3*BCN//BAV92/3/TILHI/5/BAV92/3/PRL/SARA//TSI/VEE#5/4/CROC_1/AE.SQU ARROSA (224)//2*OPATA
LM40	WBLL1*2/VIVITSI/6/CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*JANZ
LM41	C80.1/3*BATAVIA//2*WBLL1/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES
LM42	TRCH/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES
LM43	ROLF07*2/6/PVN//CAR422/ANA/5/BOW/CROW//BUC/PVN/3/YR/4/TRAP#1
LM44	ROLF07/TUKURU/5/WBLL1*2/4/YACO/PBW65/3/KAUZ*2/TRAP//KAUZ
LM46	FRET2/KUKUNA//FRET2/3/PARUS/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ
LM47	FRET2/KUKUNA//FRET2/3/YANAC/4/FRET2/KIRITATI
LM48	FRET2/KUKUNA//FRET2/3/PASTOR//HXL7573/2*BAU/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ
LM49	TRCH/SRTU//KACHU
LM50	HUW234+LR34/PRINIA*2//SNLG
LM51	HUW234+LR34/PRINIA*2//YANAC
LM52	HUW234+LR34/PRINIA*2//WHEAR
LM54	PBW343*2/KUKUNA*2//KITE
LM55	PBW343*2/KUKUNA//PARUS/3/PBW343*2/KUKUNA
LM56	PBW343*2/KUKUNA*2//YANAC
LM57	PBW343*2/KUKUNA//SRTU/3/PBW343*2/KHVAKI
LM58	ATTILA*2/PBW65/6/PVN//CAR422/ANA/5/BOW/CROW//BUC/PVN/3/YR/4/TRAP#1/7/ATTILA/2*PASTOR
LM59	FRET2/KUKUNA//FRET2/3/WHEAR/4/FRET2/TUKURU//FRET2
LM60	ALD/CEP75630//CEP75234/PT7219/3/BUC/BJY/4/CBRD/5/TNMU/PF85487/6/PBW343*2/KUKUNA/7/CNO 79//PF70354/MUS/3/PASTOR/4/BAV92

## Appendix 2.1 continued

<b>ENTRY</b>	<b>PEDIGREE</b>
Genotypes from CIMMYT Drought Stress Tolerance Nursery	
<b>LM71</b>	BABAX/3/PRL/SARA//TSI/VEE#5/4/CROC_1/AE.SQUARROSA (224)//2*OPATA
<b>LM72</b>	BABAX/3/PRL/SARA//TSI/VEE#5/4/WBLL1
<b>LM75</b>	BUC/MN72253//PASTOR
<b>LM76</b>	MILAN/KAUZ//PRINIA/3/BABAX
<b>LM77</b>	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*FRAME
<b>LM79</b>	CROC_1/AE.SQUARROSA (205)//BORL95/3/KENNEDY
<b>LM80</b>	CROC_1/AE.SQUARROSA (205)//KAUZ/3/SLVS
<b>LM81</b>	CROC_1/AE.SQUARROSA (224)//2*OPATA/3/2*RAC655
<b>LM82</b>	HD30/5/CNDO/R143//ENTE/MEXI75/3/AE.SQ/4/2*OCI
<b>LM83</b>	PASTOR/3/VEE#5//DOVE/BUC
<b>LM84</b>	SRN/AE.SQUARROSA (358)//MILAN/SHA7
<b>LM85</b>	SW94.60002/4/KAUZ*2//DOVE/BUC/3/KAUZ/5/SW91-12331
<b>LM86</b>	CHAM 6
<b>LM90</b>	CROC_1/AE.SQUARROSA (205)//BORL95/3/KENNEDY-2
<b>LM91</b>	FRTL/CMH83.2517
<b>LM93</b>	PASTOR/FLORKWA.1//PASTOR
<b>LM96</b>	ALTAR 84/AE.SQ//2*OPATA/3/PIFED
<b>LM97</b>	KRICHAUFF/2*PASTOR
<b>LM98</b>	KABY//2*ALUBUC/BAYA
<b>ENTRY</b>	<b>PEDIGREE</b>
<b>LM99</b>	ALTAR 84/AEGILOPS SQUARROSA (TAUS)//OCI/3/VEE/MJI//2*TUI
<b>LM100</b>	SW89.5277/BORL95//SKAUZ
<b>Checks</b>	
<b>LM70</b>	Check
<b>BW80</b>	Check
<b>BW100</b>	Check
<b>BW120</b>	Check
<b>BW140</b>	Check

<sup>a</sup>Mathew et al., (2019)

### Chapter 3: Path Coefficient and Principal Component Analyses for Biomass Allocation, Drought Tolerance and Carbon Sequestration Potential in Bread Wheat (*Triticum aestivum* L.)

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#### Abstract

Increased root biomass allocation could serve as a secondary trait for selecting crop ideotypes with drought tolerance and carbon sequestration potential in agricultural soils. The objective of this study was to estimate the magnitude of the relationship between root biomass and yield components and to identify influential traits to optimise genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat (*Triticum aestivum* L.). One-hundred wheat genotypes consisting of 10 parents and 90 derived F<sub>2</sub> families were evaluated under drought-stressed and non-stressed conditions at two different sites. Data were collected for days to heading (DTH), days to maturity (DTM), plant height (PH), productive tiller number (TN), spike length (SL), spikelets per spike (SPS), kernels per spike (KPS), thousand kernel weight (TKW), shoot biomass (SB), root biomass (RB), total plant biomass (PB), root-to-shoot ratio (RS) and grain yield (GY). There was significant ( $p < 0.05$ ) genetic variation in most assessed traits, TN and RS being exceptions. Root biomass had significant positive correlations with grain yield under drought-stressed ( $r = 0.28$ ) and non-stressed ( $r = 0.41$ ) conditions, but no significant correlation was recorded for RS and GY. Notably, both root biomass and shoot biomass had significant positive correlations under both water regimes, revealing the potential of increasing both traits with minimal biomass trade-offs. The highest positive direct effects on grain yield were found for KPS and PB under both water regimes. The present study demonstrated that selection based on KPS and PB rather than RS will be more effective in ideotype selection of segregating populations for drought tolerance and carbon sequestration potential.

**Keywords:** *Biomass allocation; Drought tolerance; Path analysis; Principal component analysis; Selection efficiency; Wheat*

### 3.1 Introduction

Soil organic carbon (SOC) is an essential component of soil health, affecting the chemical, physical and biological properties of agricultural soils. In Sub-Saharan Africa (SSA), soils of most agricultural lands are degraded due to high soil carbon loss driven by intensive production, poor soil management and crop residue removal (Corbeels et al., 2019). Crop residues present the largest source of carbon (45%) that can be assimilated into the soil through carbon sequestration to improve SOC content (Lal 1997). The source of crop residues are root biomass or above-ground plant biomass. However, subsoil additions of carbon from root residues in the form of root litter and root exudates are more efficient in increasing SOC than above-ground plant residues (Chenu et al., 2019). Furthermore, the residence time in soil of root-derived carbon is 2.4 times that of carbon derived from shoot biomass (Rasse et al., 2005; Kätterer et al., 2011). Hence, soil carbon derived from root biomass is critical for the long-term stabilisation of soil carbon stocks. Promoting below-ground additions of carbon via increased crop root biomass may improve the rate of carbon sequestration in agricultural soils (Hirte et al., 2018a).

Breeding wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ , AABBDD) with high biomass allocation to roots promises to increase carbon sequestration potential and contribute to yield stability in dryland farming (Kell 2011). Crops grown under dryland or rainfed systems are exposed to high fluctuations of water in the soil profile due to rainfall variability and recurrent drought. Plants respond to these fluctuations by altering their biomass allocation patterns (Dolezal et al., 2021). The most unique mechanism by which plants adjust biomass allocation under drought stress is by increasing root-to-shoot ratios, whereby plants allocate more carbohydrates to roots (McCarthy and Enquist 2007). The accumulation of carbohydrates in the roots stimulates more profound root growth as plants scavenge for moisture to support growth and development (Eziz et al., 2017). Different studies have shown that root sizes and depths vary significantly within species and between crop cultivars of major cereals, including wheat (Lin et al., 2019), maize and rice (Verma et al., 2019). This genetic variation allows for the identification of contrasting parental genotypes with optimal growth and biomass allocation and agronomic traits to generate new breeding populations for the development of wheat ideotypes with high root biomass and better yield gains. There is a dearth of information and some debate about whether large root systems impact the increased productivity of wheat in different soil moisture conditions (Palta et al., 2011; Figueroa-

Bustos et al., 2018). Root biomass has been regarded as an inefficient sink for photo-assimilates, as twice the amount of carbohydrates needed to produce one unit of shoot biomass is needed to produce one unit of root biomass (Fang et al., 2011). In high-input crop production systems that use inorganic fertilisers and irrigation, deeper root systems are underestimated, as water and nutrients are readily available (Schneider et al., 2020). However, recent studies have shown that root system plasticity can be targeted to provide resilience and yield stability under both irrigated and rainfed conditions in arid and semi-arid environments (Lynch 2015; Hirte et al., 2018b; Friedli et al., 2019). High root biomass increases the capacity for and the efficiency of water capture from the soil profile to support plant growth, biomass production, anthesis, grain filling and final grain yield (Manschadi et al., 2006). Figueroa-Bustos et al., (2018) reported a 25% increase in shoot biomass production under full irrigation in wheat cultivars with high root biomass relative to those with small root systems. Positive correlations have been observed between seedling root attributes and yield-promoting traits, such as maturity time, kernels per spike, shoot biomass and grain yield, in wheat (Xie et al., 2017; Bai et al., 2019). Therefore, increasing rooting capacity, yield and yield-influencing agronomic traits could stabilise productivity and ensure sustainable grain production of wheat cultivars in different soil moisture conditions (Lynch 2007; Xie et al., 2017).

The extent of the relationship between root biomass and yield components can be explored through path coefficient and principal component analyses to identify influential traits for cultivar development. In an attempt to develop next-generation wheat cultivars for drought tolerance and carbon sequestration potential, the research group at the University of KwaZulu-Natal identified lines with high genetic variation for desirable traits, such as root biomass, root-to-shoot ratio and grain yield under drought conditions. The selected lines were crossed to produce new breeding populations which were advanced to the F<sub>2</sub> generation for individual plant selection. Selected plants will be advanced to subsequent generations via pure line or pedigree breeding using complementary technologies, such as doubled haploidy and speed breeding to fast-track selection gains (Dwivedi et al., 2015; Yan et al., 2017). In light of the above background, the objective of this study was to assess the magnitude of the relationship between root biomass and yield components and identify influential traits to optimise selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat. Evaluations of the parental lines and F<sub>2</sub> families were conducted in field and greenhouse trials. It was hypothesized that there are direct or indirect relationships between and variable contributions made by root biomass and

above-ground traits, this hypothesis being used as a guide in the selection of unique genotypes with high root biomass and better grain yield.

### 3.2 Materials and methods

#### 3.2.1 Plant material and population development

The study used 10 contrasting wheat parental lines selected based on their genetic variation for grain yield and better shoot and root biomass production under drought conditions. The names and pedigrees of the parental genotypes are summarised in Table 3.1. Eight of the lines were candidate drought- and heat-tolerant lines acquired from the International Maize and Wheat Improvement Center's (CIMMYT) drought and heat nurseries, and two of the lines were South African local checks adapted to dryland wheat production. The parents were crossed in controlled environment facilities (CEFs) at the University of KwaZulu-Natal (UKZN), South Africa. The parental lines were stagger-planted on three occasions with two-week intervals to allow for synchronised flowering for emasculation and pollination. A total of 90 F<sub>1</sub> crosses were developed, including 45 direct crosses and 45 reciprocals using a full diallel mating design. The F<sub>1</sub> seeds were harvested and bulked, and advanced to the F<sub>2</sub> generation. The 10 parental lines and their 90 F<sub>2</sub> families were evaluated under field and greenhouse conditions, as described below.

Table 3.1. Names and pedigrees of bread wheat parental lines used in a full diallel crosses

ENTRY	PEDIGREE	DSI
<b>BW140</b>	Check	0.28 <sup>a</sup>
<b>BW141</b>	CGSS05B00243T-099TOPY-099M-099NJ-099NJ-1WGY-0B	0.40 <sup>a</sup>
<b>BW152</b>	CGSS05B00258T-099TOPY-099M-099NJ-1WGY-0B	0.25 <sup>a</sup>
<b>BW162</b>	CGSS05B00304T-099TOPY-099M-099NJ-099NJ-3WGY-0B	0.41 <sup>a</sup>
<b>LM26</b>	ATTILA*2/PBW65//TAM200/TUI	0.24 <sup>a</sup>
<b>LM47</b>	FRET2/KUKUNA//FRET2/3/YANAC/4/FRET2/KIRITATI	0.29 <sup>a</sup>
<b>LM48</b>	FRET2/KUKUNA//FRET2/3/PASTOR//HXL7573/2*BAU/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/ TRAP//KAUZ	0.32 <sup>a</sup>
<b>LM70</b>	Check	0.27 <sup>a</sup>
<b>LM71</b>	BABAX/3/PRL/SARA//TSI/VEE#5/4/CROC_1/AE.SQUARROSA (224)//2*OPATA	0.40 <sup>a</sup>
<b>LM75</b>	BUC/MN72253//PASTOR	0.38 <sup>a</sup>

\* = backcross, DSI = drought sensitivity index, <sup>a</sup>Mathew et al., (2019)

### 3.2.2 Phenotyping for root biomass and yield components

#### 3.2.2.1 Field evaluation

##### Experimental design and planting

The test genotypes (10 parental lines and 90 F2 families) were planted in the field at Ukulinga Research Farm of the University of KwaZulu-Natal (29° 40' S, 30° 24' E; 806 m above sea level). The trial was laid out in a 10 × 10 alpha lattice design with two replications. Genotypes were planted on a 2 m-long plot spaced 30 cm apart, and plants were spaced 20 cm within the row. Three seeds were planted per hole in the experimental unit and thinned to two plants per hill after two weeks of germination. Border rows were used to reduce the risk of yield inflation in test plots in the outer rows. Water and fertiliser were applied through an automated drip irrigation system to ensure that all plants received equal amounts of water.

##### Imposing drought stress

The trial was conducted under two water regimes (drought-stressed and non-stressed conditions). Drought-stress was imposed at heading growth stage (Zadoks et al., 1974) by withholding irrigation until soil moisture dropped to 35% field capacity, followed by re-watering to 80% field capacity. The non-stressed treatment received water by an automated drip irrigation system to maintain the soil at 80% field capacity. The soil moisture content was monitored by digital moisture sensors (HOBO UX120, Onset, USA) inserted to a depth of 60 cm and placed in each replicate of the different water regimes. Standard agronomic practices were used in both water regimes for the duration of the trials according to wheat production guidelines in South Africa (DAFF, 2016). Weather data were recorded for the duration of growth during the trial and are summarised in Table 3.2.

Table 3.2. Monthly weather data during the field trial at Ukulinga Research Farm, Pietermaritzburg, South Africa (2020)

Month	Max Temp (°C)	Min Temp (°C)	Humidity (%)	Rainfall (mm)
July	19.9	5.4	60	31
August	21.8	7.7	60	37
September	23.1	10	67	59
October	23.3	12	75	100
November	23.7	13.5	79	121
December	24.8	15.3	81	137

Max Temp = average maximum temperature, Min Temp = average minimum temperature

### **3.2.2.2 Greenhouse evaluation**

A greenhouse trial was established at the CEF at the UKZN in Pietermaritzburg, South Africa. The temperature inside the greenhouse was maintained at 25 °C during the day and 15 °C at night. The experimental design followed that of the field evaluation. Plants were grown in 10 L-capacity plastic pots filled with composted pine bark. Eight seeds were planted in each pot and thinned to five seedlings at two weeks after germination. Water and fertiliser were supplied as described in Section 3.2.2.1.

#### **Imposing drought stress**

The trial was conducted under drought-stressed and non-stressed conditions. Irrigation was withheld at the heading stage in the drought-stressed treatment to impose water stress. Re-watering to 80% of field capacity was initiated when moisture dropped to 35% of field capacity to avoid total crop failure. The non-stressed treatment received irrigation four times a day until crop maturity to maintain growing media at 80% of field capacity. Aphids and powdery mildew were chemically controlled using Chess (active ingredient: pyridine azomethine) and Tilt (active ingredient: triazole), respectively. Any emerging weeds were removed manually.

### **3.2.3 Data collection**

During both field and greenhouse evaluations, data were collected on root biomass, biomass traits and yield components. Days to heading were recorded as the number of days from planting to when 50% of the genotypes in each test plot had fully exposed spikes; days to maturity were recorded as the number of days from planting to when 50% of the genotypes in each test plot had dried spikes; plant height was measured as the height of the plant from the soil to the tip of the spike in centimeters (cm); productive tiller number was recorded as the number of tillers with spikes containing grain at harvest; spike length was the length of the spike excluding the awns and expressed in cm; the number of spikelets per spike was counted as the number of spikelets per individual spike; the number of kernels per spike was counted and represented the number of kernels harvested from an individual spike; and thousand kernel weight was taken as the weight of 1,000 kernels randomly selected from a genotype and weighed in grams (g). Shoot biomass was recorded as the total above-ground biomass cut from the base of the plant, excluding the grain. The shoots were oven-dried at 70 °C for 48 h, weighed and expressed in g m<sup>-2</sup>. Root biomass was recorded as the total root dry matter harvested per genotype per plot. Root samples for each plot

were harvested to a depth of 50 cm. Large roots were separated from the soil by hand and washed under running water to remove all soil particles. The remaining soil was mixed with water and the suspension was sieved through a 2 mm sieve. Fine roots were collected from the sieve residue and added to the large roots. The roots were oven-dried at 70 °C for 48 h. The dried roots were weighed on a balance to obtain the root biomass, which was adjusted to  $\text{g m}^{-2}$ . Total plant biomass was the sum of all dry plant material for each genotype, including root biomass, shoot biomass and grain yield, harvested from the test plots and recorded in  $\text{g m}^{-2}$ . Root-to-shoot ratio was the ratio of the root biomass to the shoot biomass, as recorded above. Grain yield was the weight of harvested grain at 12.5% moisture content per genotype per plot and expressed in  $\text{gm}^{-2}$ .

### **3.2.4 Data analysis**

The data collected across the two sites were individually analysed and subjected to Bartlett's test of homogeneity test of variance. A combined analysis of variance (ANOVA) was done to test genotype effects using a lattice procedure involving a three-way interaction of genotype, water regime and site, using Genstat 18th Edition (Payne et al., 2017). Mean values of the test genotypes for the assessed traits were compared at the 5% significance level using Fisher's least significance difference (LSD) procedure. Pearson's correlation coefficients ( $r$ ) were calculated separately for drought-stressed and non-stressed conditions using Genstat 18th Edition (Payne et al., 2017). Correlation coefficients were partitioned into direct and indirect effects using the phenotypic correlation matrix:  $A = B \times C$ , where A stands for the phenotypic correlation coefficients of grain yield with yield components and root attributes, B refers to the phenotypic correlations among all the recorded traits in all combinations, and C is the value of the path coefficients. The inverse of matrix B was calculated in Microsoft Excel 2016, using the Matrix Inverse function (MINVERSE). The direct and indirect path coefficients of yield components and root biomass were calculated as the products of phenotypic correlations and inverse matrix B, according to (Dewey and Lu 1959). Path coefficient analysis diagrams were developed in R software using structural equation modelling (R Core Team, 2020). The rotated component matrix and principal component analysis (PCA) biplots were generated for yield components and root biomass based on the correlation matrix in Genstat 18th Edition. Both analyses were separated for drought-stressed and non-stressed conditions.

### **3.3 Results**

#### **3.3.1 Analysis of variance**

The combined analysis of variance revealed significant differences among the test genotypes for the recorded traits, except for TN and RS (Table 3.3). There were significant differences for RS, TN, DTH, SPS, TKW, spike length and grain yield due to the genotype-by-water regime interaction effect. Significant differences were recorded for DTH, SPS, KPS, TKW, PB, plant height, spike length, shoot biomass, root biomass and grain yield for the genotype-by-site interaction. The genotype-by-water regime-by-site interaction effect was significant only for spike length, SPS and TKW.

Table 3.3. Combined analysis of variance and significant tests for yield components and root attributes of 10 parental lines and their 90 F<sub>2</sub> progenies evaluated under drought-stressed and non-stressed conditions across two sites

SOV	d.f	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	SB	RB	PB	RS	GY
<b>Replication</b>	1	30.06	228.44***	142.45	335.34***	5.95*	18.01*	212.15	421.16***	4484.00	10390.90***	220237.00*	0.49***	43869.00*
<b>Block</b>	18	29.41***	27.11	176.89*	21.30	2.06*	6.352	115.63*	56.25**	25982.00***	994.50*	67304.00	0.04	21502.00**
<b>Genotype (Gen)</b>	99	60.16***	41.60***	243.27***	16.10	4.09***	11.61***	142.25***	58.08***	18128.00***	769.50**	69654.00***	0.02	14638.00**
<b>Water Regime (WR)</b>	1	36.23	11794.04***	11091.44***	205.42**	59.49***	202.55***	7189.67***	9737.33***	938657.00***	10709.50***	12251041.00***	1.68***	5465271.00***
<b>Site</b>	1	46292.11***	128227.14***	89648.69***	15460.90***	1630.17***	5094.70***	67179.66***	64551.23***	2054036.00***	24588.50***	1132252.00***	0.05	165356.00***
<b>Gen*WR</b>	99	13.34*	20.84	104.61	20.34*	1.59*	7.20***	71.70	32.42*	11642.00	631.90	53980.00	0.03*	13481.00*
<b>Gen*Site</b>	98	37.36***	17.86	149.27***	17.57	2.28***	10.32***	94.62*	32.11*	17491.00***	756.10*	67155.00**	0.03	14496.00*
<b>Gen.WR.Site</b>	97	12.37	17.73	116.64	13.40	1.73**	7.13***	72.21	37.09***	12166.00	577.70	45619.00	0.03	12154.00
<b>Residual</b>	368	9.79	19.02	91.79	14.67	1.148	4.352	66.81	23.58	10071.00	533.00	43026.00	0.03	10167.00

SOV = source of variation, df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>)

### 3.3.2 Mean performance

The mean values of measured traits of the ten best performing genotypes and the lowest-performing genotypes based on grain yield under drought-stressed conditions are presented in Appendix 3.1. Genotype LM70 × BW141 had the fewest days to heading under drought-stressed and non-stressed conditions. Three of the top four genotypes (LM26 × BW140, BW140 × LM71 and LM47 × BW152) matured later when compared with the lowest-performing genotypes. The top ten genotypes were generally taller than the lowest performing genotypes, while no clear trends were found for TN for the two groups. Spike length (6.13%) and SPS (5.82%) were reduced slightly by drought stress. Among the lowest-performing genotypes, BW152 (399.15 g m<sup>-2</sup>) and BW162 × LM71 (334.12 g m<sup>-2</sup>) had higher shoot biomass under non-stressed conditions than all the top 10 genotypes. However, these values were significantly reduced under drought-stressed conditions. LM75 × LM71 had notably high shoot biomass (>300 g m<sup>-2</sup>), root biomass (>40 g m<sup>-2</sup>) and PB (>400 g m<sup>-2</sup>) values under both moisture conditions but it had low yield gain (72.11 g m<sup>-2</sup>) under drought. For all genotypes, the average root-to-shoot ratio increased by 60% due to drought stress. The lowest-performing genotypes had relatively high grain yields (> 300 g m<sup>-2</sup>) under non-stressed conditions. Among the top-performing genotypes, only genotype BW162 × LM75 (436.16 gm<sup>-2</sup>) had a higher grain yield under non-stressed conditions than all of the poor-performing genotypes.

### 3.3.3 Principal component and biplot analyses

The rotated component matrix showing the percentage variance of different principal components (PCs) and the respective loadings of recorded traits is shown in Table 3.4. The first four PCs with eigenvalues greater than one under non-stressed conditions had a cumulative variance of 79.93%. The first PC had the highest variation of 37.04%, followed by PC2 with 15.27%. Shoot biomass, PB and grain yield made the highest contributions to PC1, followed by root biomass, RS and TKW with positive contributions to PC2. The highest positive loadings for PC3 and PC4 were for RS and DTM, respectively. Under drought-stressed conditions, the first PC had a percentage variance of 39.19% and was positively correlated with PB, shoot biomass, SPS, spike length and plant height. The second and third PCs were correlated with DTH and TKW, respectively. Principal components 4 and 5 had high positive loadings for root-related traits such as RS and root biomass, respectively.

Biplots based on the principal component analysis were drawn for drought-stressed and non-stressed conditions (Figures 3.1 and 3.2, respectively). The genotypes were evenly scattered across both PC1 and PC2 under drought-stressed conditions. High-yielding genotypes under stress such as the parental line LM75 and cross BW140 × LM71 had high KPS and PB, while LM26 × BW140 and LM47 × BW152 were also associated with TN (Figure 3.1 and Appendix 3.1). High RS and late flowering were reflected in poor-yielding families including LM47 × LM71, LM75 × LM71 and BW152 (Figure 3.1 and Appendix 3.1). Under non-stressed conditions, grain yield had strong correlations with PB and TN, and high-yielding genotypes under these moisture conditions, including crosses LM71 × LM75 and LM71 × LM26, which excelled in these traits (Figure 3.2 and Appendix 3.1).

Table 3.4. Rotated component matrix for 13 yield components and root attributes in 100 wheat genotypes assessed under drought-stressed and non-stressed conditions

Traits	Non-stress				Drought-stress				
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC5
<b>DTH</b>	0.08	-0.38	0.17	-0.33	0.05	0.44	0.35	0.22	0.33
<b>DTM</b>	0.06	-0.29	0.01	0.45	-0.11	-0.49	0.18	0.34	0.27
<b>PH</b>	0.32	0.00	0.25	-0.29	0.35	0.07	0.33	0.07	0.10
<b>TN</b>	0.29	0.25	-0.27	0.04	0.26	-0.09	-0.30	-0.25	0.26
<b>SL</b>	0.32	-0.24	0.36	-0.12	0.35	0.13	0.26	0.24	-0.16
<b>SPS</b>	0.34	-0.29	0.24	0.07	0.35	0.11	0.14	0.25	-0.21
<b>KPS</b>	0.26	-0.37	0.03	0.22	0.27	-0.16	0.00	0.14	-0.60
<b>TKW</b>	0.04	0.31	0.24	-0.56	-0.18	-0.37	0.42	0.20	0.25
<b>SB</b>	0.39	0.07	-0.28	-0.05	0.39	0.06	0.05	-0.20	0.23
<b>RB</b>	0.22	0.43	0.28	0.28	0.27	0.04	-0.43	0.25	0.39
<b>PB</b>	0.41	0.16	-0.21	0.04	0.39	-0.22	-0.06	-0.09	0.19
<b>RS</b>	-0.04	0.31	0.60	0.37	-0.08	0.07	-0.44	0.69	-0.03
<b>GY</b>	0.39	0.14	-0.19	0.05	0.23	-0.55	-0.05	-0.02	-0.10
<b>Eigenvalue</b>	4.82	1.99	1.40	1.35	5.10	1.79	1.52	1.23	1.02
<b>Percentage variance (%)</b>	37.04	15.27	10.74	10.35	39.19	13.77	11.66	9.45	7.81
<b>Cumulative variance (%)</b>	37.04	52.31	63.05	73.40	39.19	52.96	64.62	74.07	81.88

PC = principal component, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = tiller number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, SB = shoot biomass, RB = root biomass, PB = total plant biomass, RS = root to shoot ratio, and GY = grain yield

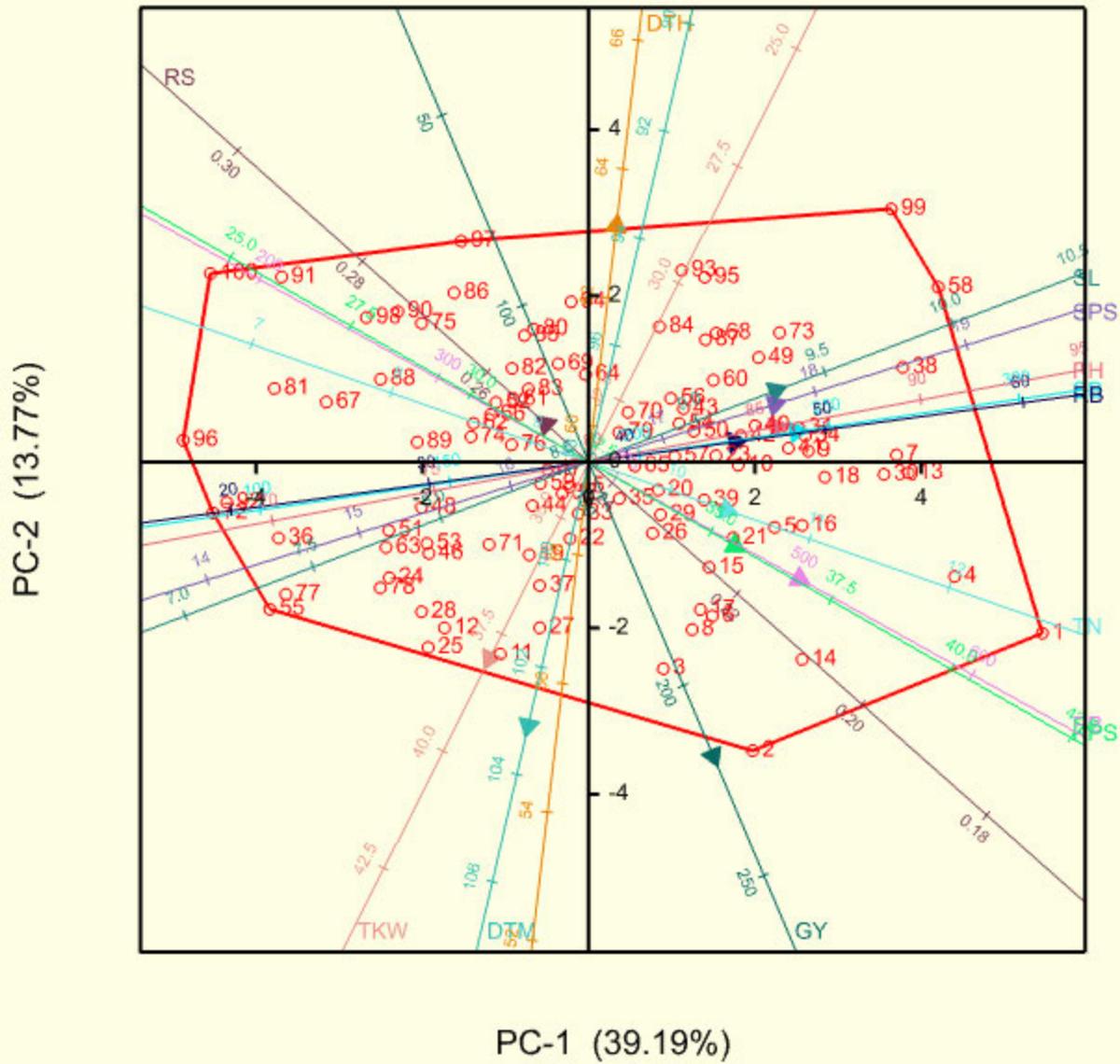


Figure 3.1. Principal component biplot under drought-stressed conditions of 10 bread wheat parental lines and 90  $F_2$  families. Genotypes are coded in numbers as recorded in Appendix 1.1. Smaller angles between vectors of recorded traits indicate a high correlation between the traits in discriminating genotypes. Genotypes plotted closer to and further along a vector line scored highly in that particular trait. PC = principal component, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass ( $g\ m^{-2}$ ), RB = root biomass ( $g\ m^{-2}$ ), PB = total plant biomass ( $g\ m^{-2}$ ), RS = root to shoot ratio and GY = grain yield ( $g\ m^{-2}$ )

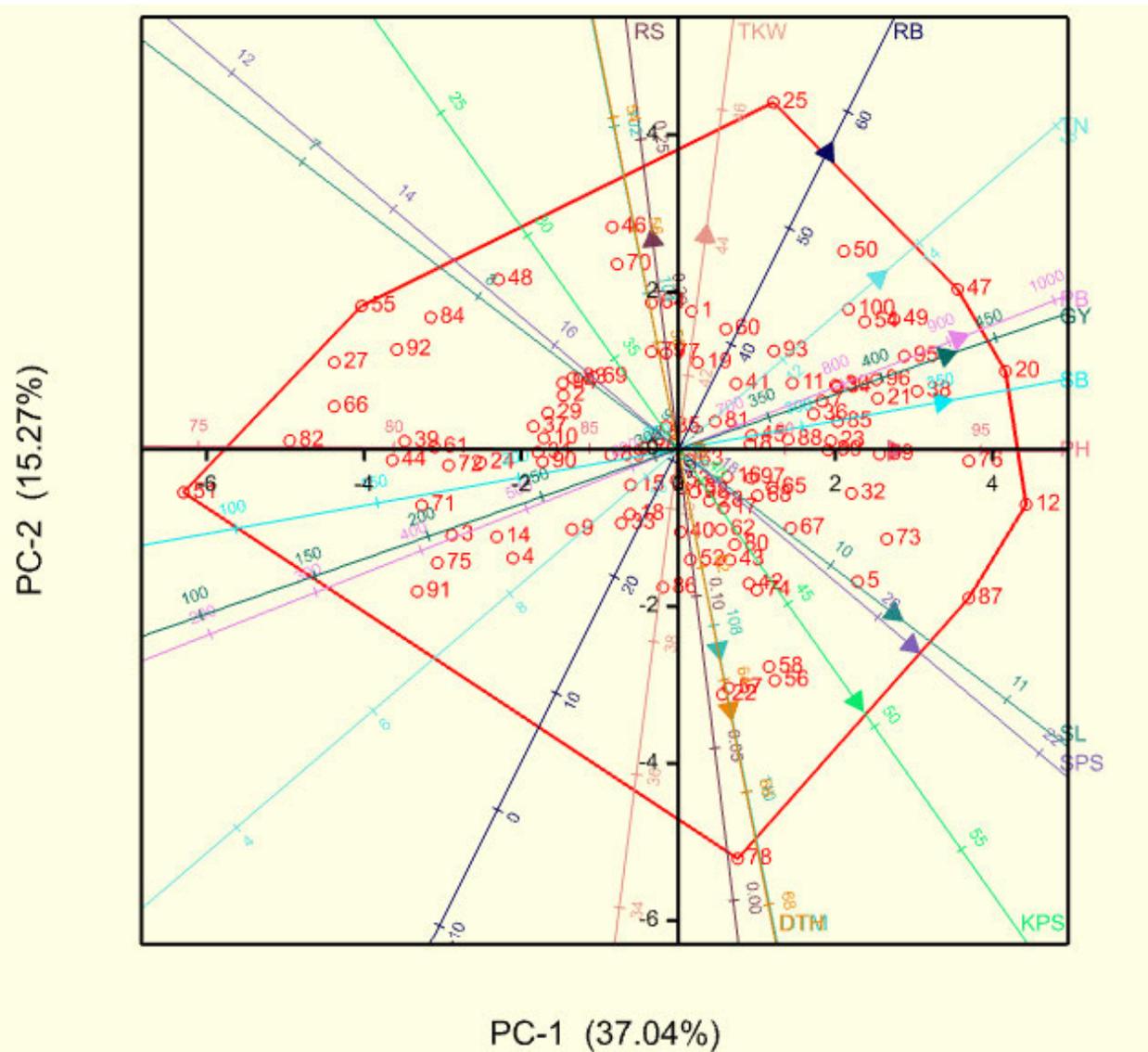


Figure 3.2. Principal component biplot under non-stressed conditions of 10 bread wheat parental lines and 90 F<sub>2</sub> families. Genotypes are coded in numbers as recorded in Appendix 1.1. Smaller angles between vectors of recorded traits indicate a closer relationship between the traits in discriminating genotypes. Genotypes plotted closer to and further along a vector line scored highly in that particular trait. PC = principal component, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>)

### **3.3.4 Correlations of root biomass and yield components with grain yield under drought-stressed and non-stressed conditions**

Phenotypic correlation coefficients showing the relationships between root attributes and yield components under drought-stressed and non-stressed conditions are shown in Table 3.5. Grain yield showed higher positive correlations with PB ( $r = 0.67$ ) and KPS ( $r = 0.55$ ) under drought-stressed conditions. Productive tiller number and shoot biomass had moderate correlations with grain yield of  $r = 0.33$  and  $r = 0.39$ , respectively, whereas root biomass had low ( $r < 0.30$ ) positive correlations with grain yield. Only DTH had significant negative correlations ( $r = -0.38$ ) with grain yield. Root biomass was positively correlated with RS and all above-ground traits except DTH and DTM. Negative correlations were recorded for RS with plant height ( $r = -0.24$ ), shoot biomass ( $r = -0.31$ ) and PB ( $r = -0.19$ ).

Table 3.5. Simple correlation coefficients and significance tests for yield components and root attributes of 10 bread wheat parental lines and 90 F<sub>2</sub> progenies under drought-stressed (lower diagonal values) and non-stressed (upper diagonal) conditions at two sites

Traits	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	SB	RB	PB	RS	GY
<b>DTH</b>	1	0.03	0.23*	-0.05	0.21*	0.13	0.12	0.02	0.10	-0.16	0.03	-0.17	0.02
<b>DTM</b>	-0.29**	1	-0.01	-0.01	0.05	0.32**	0.05	-0.21*	0.11	0.03	0.03	-0.01	0.02
<b>PH</b>	0.28**	-0.25*	1	0.32**	0.55***	0.51***	0.28**	0.32**	0.53***	0.31**	0.51***	-0.05	0.48***
<b>TN</b>	-0.04	-0.10	0.30**	1	0.22*	0.24*	0.15	0.05	0.59***	0.42***	0.62***	0.03	0.60***
<b>SL</b>	0.27**	-0.27**	0.74***	0.31**	1	0.76***	0.49***	0.10	0.45***	0.22*	0.41***	-0.06	0.41***
<b>SPS</b>	0.13	-0.15	0.64***	0.32**	0.79***	1	0.62***	-0.04	0.49***	0.20	0.47***	-0.07	0.48***
<b>KPS</b>	-0.04	-0.06	0.39***	0.25*	0.49***	0.55***	1	-0.25*	0.29**	0.04	0.40***	-0.11	0.48***
<b>TKW</b>	-0.13	0.37***	-0.17**	-0.22*	-0.24*	-0.38***	-0.29**	1	0.05	0.09	0.10	0.08	0.13
<b>SB</b>	0.15	-0.23*	0.71***	0.55***	0.63***	0.59***	0.41***	-0.40***	1	0.37***	0.84***	-0.24*	0.72***
<b>RB</b>	0.06	-0.03	0.37***	0.51***	0.36***	0.40***	0.23*	-0.33***	0.58***	1	0.49***	0.65***	0.41***
<b>PB</b>	-0.06	-0.03	0.60***	0.57***	0.54***	0.58***	0.50***	-0.26**	0.88***	0.64***	1	-0.05	0.94***
<b>RS</b>	0.03	0.10	-0.24*	-0.06	-0.13	-0.13	-0.11	-0.05	-0.31**	0.39***	-0.19***	1	-0.03
<b>GY</b>	-0.38***	0.24*	0.26**	0.33***	0.24*	0.25*	0.55***	0.09	0.39***	0.28**	0.67***	-0.14	1

\* significant at  $P < 0.05$ ; \*\*  $P < 0.01$ , DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ), RS = root to shoot ratio and GY = grain yield ( $\text{g m}^{-2}$ )

### 3.3.5 Path coefficient analysis of root biomass and yield components on grain yield

Direct and indirect effects of yield components and root attributes on grain yield under drought-stressed and non-stressed conditions are summarised in Appendix 3.2 and Figure 3.3 and Appendix 3.3 and Figure 3.4, respectively. PB (1.001) had the greatest direct effect on grain yield under drought-stressed conditions, followed by KPS (0.34) and TKW (0.17). Conversely, shoot biomass and root biomass had negative direct effects on grain yield at  $-0.410$  and  $-0.153$ , respectively. Shoot biomass (0.88) and root biomass (0.65) had the greatest positive indirect effects on grain yield through PB. Indirect effects on grain yield through PB were observed for plant height, TN, spike length, SPS and KPS. Root-to-shoot ratio had negative direct effects on grain yield through PB.

Under non-stressed conditions, PB (1.06) and KPS (0.13) had positive direct effects on grain yield. Shoot biomass ( $-0.19$ ) and root biomass ( $-0.13$ ) had negative direct effects on grain yield; however, the same traits had large positive indirect effects of 0.89 and 0.52, respectively, on grain yield through PB. Except for RS, the assessed traits had positive indirect effects on grain yield through PB, and including plant height (0.55), TN (0.66), spike length (0.44), SPS (0.50) and KPS (0.43). The residual value for the path analysis model was 0.077 under drought-stressed conditions and 0.231 under non-stressed conditions (Figures 3.3 and 3.4).

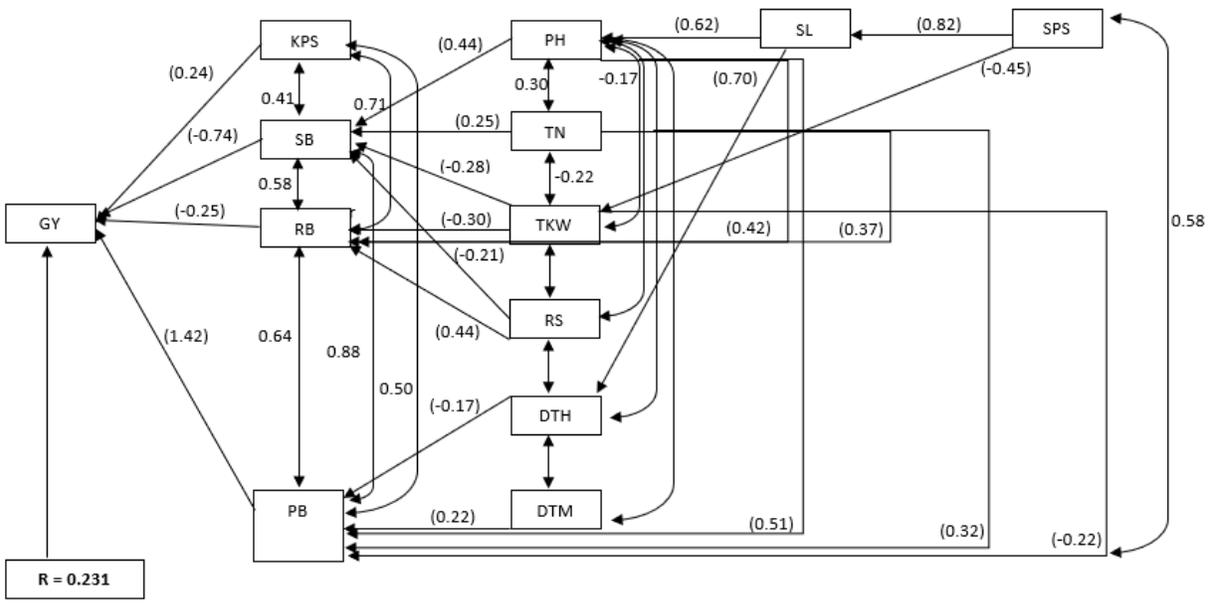


Figure 3.3. Path analysis model diagram displaying causal relationships of assessed traits on grain yield in 10 bread wheat parental lines and 90 derived  $F_2$  families of wheat assessed under drought-stressed conditions. Values in parenthesis are direct path coefficients, while other values are correlation coefficients. R = residual effect; DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = Thousand kernel weight (g), SB = shoot biomass ( $g\ m^{-2}$ ), RB = root biomass ( $g\ m^{-2}$ ), PB = total plant biomass ( $g\ m^{-2}$ ), RS = root to shoot ratio, and GY = grain yield ( $g\ m^{-2}$ )

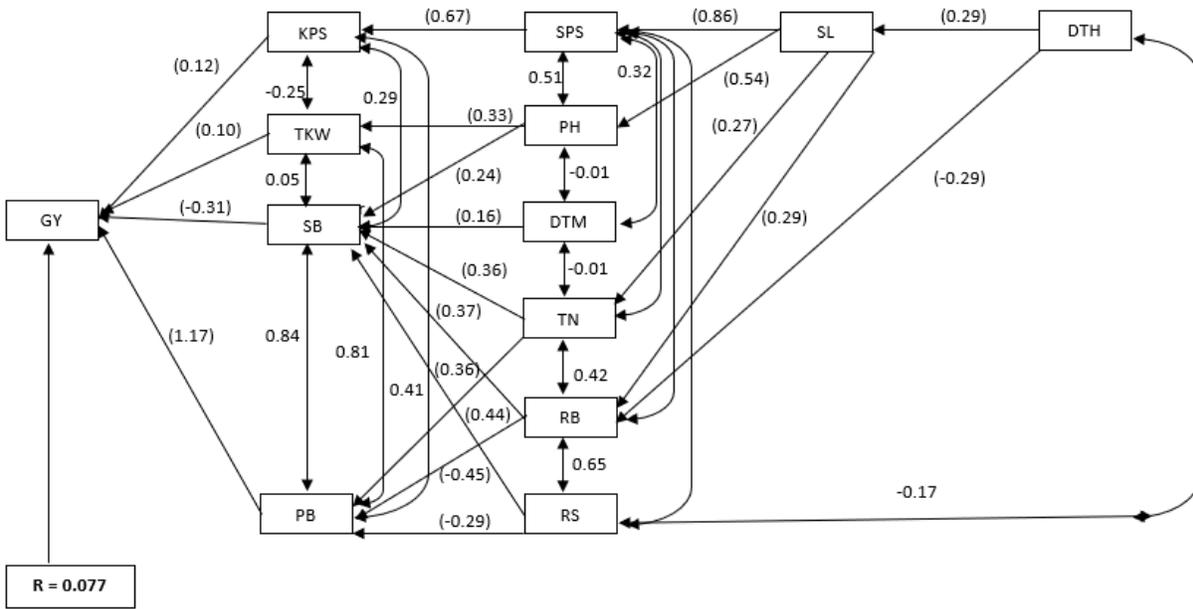


Figure 3.4. Path analysis model diagram displaying causal relationships of assessed traits on grain yield in 10 bread wheat parental lines and 90 derived  $F_2$  families of wheat assessed under non-stressed conditions. Values in parenthesis are direct path coefficients while other values are correlation coefficients. R = residual effect; DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = Thousand kernel weight (g), SB = shoot biomass ( $g\ m^{-2}$ ), RB = root biomass ( $g\ m^{-2}$ ), PB = total plant biomass ( $g\ m^{-2}$ ), RS = root to shoot ratio, and GY = grain yield ( $g\ m^{-2}$ )

### 3.4 Discussion

The genotypic differences observed for yield components and root biomass under different environments indicate sufficient genetic variation for the development of new wheat ideotypes for grain production and carbon sequestration. The rotated component matrix showed that PB, shoot biomass and grain yield were the most discriminating traits under non-stressed conditions, followed by root biomass, RS and TKW. Therefore, identifying genotypes based on biomass production and allocation will allow more effective explanation of the differences among individual genotypes and families. Similarly, under drought-stressed conditions, biomass production, as shown by high contributions of PB, shoot biomass and spike-related traits such as SPS and spike length, were the most essential traits in differentiating the test genotypes.

Positive correlations were found between shoot biomass and grain yield under both drought-stressed and non-stressed conditions, indicating the importance of shoot biomass for improving grain yield. High shoot biomass contributes to grain yield by providing greater leaf area for light interception and carbon assimilation to support grain filling (Reynolds et al., 2005; Shamuyarira et al., 2022). This agrees with Chen et al., (2019), the authors of which reported that yield gains in wheat are influenced by biomass production and sink size, which is determined by the number of fertile spikes per unit area. To increase the number of fertile spikes per unit area, breeders need to identify plant genotypes with high TN (Bastos et al., 2020). The importance of TN was notable under drought-stressed conditions, as high yielding genotypes such as LM75 and BW140 x LM71 were strongly correlated with TN. Therefore, increasing shoot biomass and TN will have a positive impact on grain yield.

The positive relationship of root biomass and grain yield shows the importance of root traits for increasing productivity under both drought-stressed and non-stressed conditions. Increase in root size improves the capacity and efficiency of nutrient and moisture acquisition by plants, increasing the resilience of agro-ecosystems. This is more important under drought conditions, where there is limited water in the soil profile and a deeper and more abundant root system can forage for water in the soil profile (Figueroa-Bustos et al., 2019). Though larger root systems in crops are important, especially in dry areas, they may, in some cases, be inefficient or even entail a yield penalty in wet seasons or in regions with sufficient water and capacity to supply supplementary irrigation (Středa et al., 2012; Fang et al., 2017). However, evidence from this study reflects that root biomass has a

positive influence on productivity, even under conditions of sufficient water availability. This is supported by Severini et al., (2020), who reported that deeper and more profuse root growth can be attained without any adverse effect on grain yield. These increased root sizes can be harnessed to increase soil carbon in agricultural soils.

Root-to-shoot ratio was negatively correlated with plant height, shoot biomass and PB under drought, which agrees with reports of Qi et al., (2019), who observed negative correlations between root-to-shoot ratio and plant height and above-ground biomass. Some studies debated this and have reported carbon trade-offs between root and shoot biomass, leading to reduced wheat productivity (Ma et al., 2010; Chang et al., 2016; Bacher et al., 2021). Therefore, increasing RS alone in pursuit of higher carbon inputs may have a negative impact on grain yield, as reflected in families such as LM47 x LM71, LM75 x LM71 and parental line BW152, which had high RS values but low yields. On the other hand, PB had the highest positive correlations with grain yield under both water regimes. Hence, instead of altering RS, yield gains may be obtained by increasing PB without compromising the carbon sequestration potential from the roots. Increasing root biomass and shoot biomass simultaneously to achieve high PB is possible, as reflected by positive correlations between root biomass and shoot biomass under drought-stressed and non-stressed conditions. However, shoot biomass showed stronger indirect effects on grain yield through PB than root biomass under both water regimes. This may indicate the greater contribution to grain yield by shoot biomass than by root biomass under different soil moisture environments. Increasing shoot biomass in such cases rather than root biomass may be more beneficial for yield increases but will lead to a considerable reduction in potential carbon inputs in the soil due to reduced root sizes (Lilley et al., 2011; Chenu et al., 2019).

KPS had high correlations and direct effects on grain yield under both water regimes thereby corroborating the report of Feng et al., (2018). According to Fischer (2008), KPS determines the level of grain yield that is achieved in wheat and understanding the fundamental mechanisms that influence KPS will be useful in increasing grain yield. Drought stress reduces KPS due to kernel abortion, which reduces the sink strength in the spikes and causes yield loss (Shokat et al., 2020). Thus, maintaining high kernel number as in the families LM47 x BW152 and LM70 x BW141, under drought may have a positive influence on grain yield. This explains the close relationship between KPS and dry matter accumulation in the spikes, which is reflected in the strong

correlations of KPS with spike length and SPS under both drought-stressed and non-stressed conditions (Fischer 2008; Arjona et al., 2018).

The path coefficient analysis models under non-stressed conditions had lower residual values than under drought-stressed conditions. Therefore, the model with non-stressed conditions was more effective in explaining the total variation in grain yield than that with drought-stressed conditions. Both models showed that PB and KPS can be used for efficient selection for grain yield under different soil moisture conditions while pursuing the goal of increasing carbon inputs in croplands. According to Stella et al. (2019), SOC levels in the soil are determined by land management practices, such as crop residue retention. Selecting plants with high PB will be beneficial at crop farms that practice minimum tillage and other conservation practices; shoot biomass will provide more crop residues to incorporate into the soil profile after harvest. On the other hand, larger root systems in the same plants will make a high carbon contribution to croplands, especially in areas where conventional agriculture is practised and where there is little contribution from above-ground plant residues.

### **3.5 Conclusions**

Increasing RS was not effective with respect to improving wheat productivity. The positive relationship between root biomass and shoot biomass informs the possibility of increasing both traits with minimum biomass trade-offs to develop drought-tolerant cultivars with high carbon sequestration potential. The large positive direct effects of KPS and PB on grain yield under both water regimes point to plants with high root and shoot biomass production as the crop ideotype that will be most resilient and environmentally friendly under varying moisture conditions. This was observed for high-yielding genotypes, including LM75 and BW140 × LM71 under drought-stress and LM71 × LM75 and LM71 × LM26 under non-stressed conditions. Therefore, selection based on KPS and PB rather than on RS will be more effective in ideotype selection of segregating F<sub>2</sub> populations with enhanced drought tolerance and carbon sequestration potential. Selected plants and families will be advanced using pedigree breeding to develop climate-smart cultivars for dryland farming in SSA. The study recommends further evaluations across multiple environments and test populations, and including soil carbon tests (including C change after harvesting) to develop genetic models and to guide the breeding for climate-smart wheat varieties with drought tolerance and high carbon sequestration potential.

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Appendix 3.1. Mean values of yield components and root attributes of the ten parental lines and 90 F<sub>2</sub> families of wheat based on grain yield under drought-stressed conditions

No.	Genotype	DTH		DTM		PH		TN		SL		SPS		KPS		TKW	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
1	LM75	60.75	61.25	102.00	97.75	92.58	89.03	9.56	12.56	8.64	9.08	17.50	17.50	35.54	39.96	40.53	30.64
2	LM26 x BW140	53.75	59.75	103.75	106.00	80.88	75.20	10.78	13.31	8.80	9.10	16.63	16.00	37.33	36.00	36.90	34.20
3	BW140 x LM71	55.25	57.00	103.50	99.25	78.75	76.48	8.00	9.81	8.58	8.61	16.75	16.63	41.38	39.75	37.25	35.89
4	LM47 x BW152	59.25	59.50	107.00	100.00	83.30	92.13	10.19	10.13	9.48	9.38	16.88	17.63	35.79	40.88	39.66	30.35
5	LM70 x BW152	65.25	60.50	106.25	98.25	95.45	85.00	14.25	10.31	9.95	9.75	19.13	18.13	42.63	32.25	39.97	34.45
6	LM70 x BW141	56.50	54.50	106.50	95.00	90.45	83.73	7.63	10.38	9.85	8.67	18.38	17.25	45.21	40.21	42.48	36.82
7	BW162 x LM75	60.50	63.00	102.50	96.75	94.85	92.03	10.88	9.44	9.48	9.18	17.63	18.00	39.67	38.25	41.83	31.88
8	LM75 x BW141	59.00	54.50	104.25	98.25	86.23	79.55	11.88	12.31	9.56	8.58	19.38	17.38	41.96	34.29	42.45	35.37
9	BW152 x BW141	62.25	59.75	105.50	94.25	86.55	84.90	6.83	9.38	9.55	8.99	17.88	16.63	41.83	32.83	43.83	32.26
10	LM70 x BW162	62.50	60.25	103.50	96.00	84.58	78.58	9.94	12.13	8.93	9.45	16.88	18.00	36.33	33.88	43.85	33.33
11	BW141 x LM26	55.25	56.75	108.25	104.25	89.43	75.93	11.92	8.31	10.18	8.25	18.50	16.00	36.54	37.71	43.92	35.99
12	LM48 x BW140	57.50	58.00	111.50	103.25	85.58	72.13	12.94	6.81	10.13	7.43	21.63	14.63	48.42	33.88	37.21	32.84
13	LM75 x LM47	60.25	59.75	105.75	94.75	95.75	91.15	7.13	13.06	9.80	10.00	18.25	17.50	37.25	36.00	44.99	33.77
14	LM70 x LM26	55.75	58.33	106.00	105.00	85.60	83.67	7.38	9.33	9.59	9.88	17.25	18.50	34.96	40.17	39.51	39.38
15	LM47 x BW140	61.50	58.25	108.25	99.75	86.55	79.30	11.38	11.25	9.05	8.75	17.75	16.50	34.08	34.67	41.43	34.35
16	LM26 x LM71	60.75	57.00	107.75	100.00	93.13	87.20	9.88	10.75	9.39	9.43	17.75	18.00	36.75	34.83	36.35	29.67
17	BW141 x LM75	59.25	55.25	106.75	100.50	95.43	87.18	11.56	10.50	8.55	9.00	18.13	17.13	43.54	31.79	41.58	37.10
18	BW162 x LM26	59.25	55.50	108.00	95.25	83.45	84.83	9.31	12.44	9.08	9.19	18.63	19.00	42.38	34.25	38.49	31.47
19	LM26 x BW141	54.50	56.00	105.75	99.50	90.40	71.65	11.31	6.44	8.58	8.63	17.75	16.88	41.75	38.79	40.67	31.24
20	LM71 x LM26	55.75	56.00	110.25	98.00	88.70	78.38	13.63	7.63	10.50	8.83	20.25	17.50	35.21	31.21	40.26	29.62
21	BW152 x LM75	59.75	58.25	107.25	99.00	89.28	83.60	12.41	11.63	9.70	9.00	19.00	18.75	40.67	35.46	43.69	35.41
22	LM48 x BW162	69.50	61.67	112.00	101.33	98.80	84.33	6.50	7.67	9.57	8.16	19.00	16.38	38.67	36.50	45.00	37.29
23	LM75 x BW152	60.75	63.00	105.00	96.50	93.33	82.68	12.56	10.75	9.40	9.45	18.75	17.38	41.92	37.75	42.25	37.63
24	BW152 x LM26	56.25	57.50	106.75	99.75	81.58	75.48	9.31	7.75	8.38	7.15	17.75	15.00	30.33	30.17	36.58	36.86
25	BW140 x LM75	55.75	56.25	105.25	100.75	85.55	71.70	13.94	9.94	8.00	7.60	15.75	14.38	31.63	28.96	45.75	40.19
26	BW140 x BW152	58.75	57.50	109.50	98.75	85.00	80.60	11.81	13.94	8.50	7.88	18.25	16.63	36.42	28.29	43.45	34.48
27	BW162 x BW140	55.25	56.00	103.00	102.50	75.90	73.18	9.31	12.50	6.70	7.83	12.88	14.88	33.92	30.17	37.81	34.71
28	LM75 x BW140	56.50	56.75	112.00	100.50	86.10	78.30	9.13	9.31	8.98	6.33	19.38	13.38	38.92	25.92	40.09	36.42
29	LM71 x BW140	57.25	55.50	109.25	98.25	75.78	75.58	8.75	8.81	7.38	9.56	14.25	17.63	38.08	34.46	36.08	31.32
30	BW141 x LM70	58.75	60.75	103.75	96.25	96.38	91.18	12.38	11.31	9.46	9.24	17.13	17.75	38.83	34.63	46.73	35.31

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

No.	Genotype	DTH		DTM		PH		TN		SL		SPS		KPS		TKW	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
31	LM75 x LM48	62.25	61.50	103.75	98.00	83.30	86.33	8.94	12.19	8.27	9.13	15.50	17.25	36.08	35.96	40.15	29.25
32	BW141 x BW152	61.50	59.75	111.00	100.25	99.40	82.03	12.50	7.19	9.57	8.00	18.67	16.50	38.63	33.43	39.06	31.39
33	LM75 x LM70	62.75	58.25	106.25	96.25	91.50	88.45	9.06	7.13	9.38	8.95	17.50	16.38	38.46	34.79	40.84	39.54
34	LM70 x LM47	59.25	64.25	101.50	98.75	96.28	92.75	11.94	10.06	9.63	9.50	17.88	16.75	43.67	34.25	48.34	34.76
35	LM26 x LM48	57.00	57.25	104.50	98.00	85.08	79.63	11.06	7.00	8.68	9.00	15.88	17.63	44.08	45.58	36.73	31.80
36	BW162	64.75	59.25	102.50	100.75	93.13	70.05	13.56	6.00	9.13	7.13	17.88	13.75	38.88	23.67	44.76	36.34
37	BW140 x LM70	55.25	55.50	105.00	102.00	79.50	80.60	8.38	8.50	8.80	8.95	16.50	17.25	39.46	33.92	42.24	39.23
38	LM70 x LM75	62.50	62.00	107.00	93.00	97.43	94.90	8.75	11.69	9.60	9.90	17.88	17.75	38.08	41.33	44.46	31.01
39	LM47 x LM70	63.75	63.75	104.50	102.50	85.93	85.78	8.75	11.69	8.05	8.89	14.63	16.38	28.33	31.08	40.11	34.72
40	LM47 x LM48	62.00	56.25	101.25	94.50	89.30	88.68	11.19	7.88	9.85	8.95	17.38	17.38	43.17	35.25	35.35	27.73
41	LM26 x BW162	55.25	59.50	105.25	97.50	88.08	78.15	11.56	10.00	9.00	9.45	16.63	18.00	43.75	34.17	40.40	31.43
42	LM48 x LM26	62.75	61.25	107.25	97.75	82.05	76.75	12.06	10.44	9.43	8.80	18.25	17.88	51.25	37.96	37.84	30.42
43	BW162 x LM48	60.75	59.25	101.50	94.00	85.03	80.43	9.06	8.88	10.14	8.75	18.75	15.88	47.75	35.54	34.12	31.78
44	BW141	55.50	57.25	104.75	96.75	74.60	74.95	9.88	11.31	7.88	7.69	16.13	16.63	35.63	34.04	38.94	33.60
45	LM75 x BW162	63.50	57.50	106.50	95.50	89.40	81.23	12.19	13.25	9.38	8.03	18.13	15.25	34.38	30.75	44.02	34.33
46	BW140 x BW162	51.33	53.75	104.67	96.75	84.70	74.30	13.43	7.75	7.77	8.28	15.83	16.13	32.89	36.08	40.60	37.15
47	LM71 x LM75	59.75	60.75	104.25	98.00	86.15	82.08	15.75	10.19	9.15	8.30	17.63	14.75	39.29	30.79	41.01	35.63
48	LM70 x BW140	58.75	58.25	107.75	97.50	86.00	81.80	8.19	6.81	9.13	8.45	17.13	15.25	33.42	26.46	43.10	40.40
49	LM26 x LM75	62.50	60.50	104.25	94.25	91.40	86.95	13.81	12.13	8.83	9.13	17.00	16.63	37.42	33.54	42.29	28.99
50	BW162 x BW141	55.25	59.00	105.75	98.25	95.23	84.93	9.16	10.38	9.88	9.05	18.63	18.75	38.88	32.71	44.88	32.01
51	BW140 x LM48	58.25	58.50	107.50	98.25	76.40	73.25	6.13	9.19	6.63	7.38	13.13	15.00	28.75	34.04	37.84	37.82
52	LM26	59.25	56.75	103.50	95.50	83.90	69.05	10.19	7.81	9.48	8.68	17.63	17.38	44.58	41.63	35.01	29.34
53	LM48 x BW141	60.75	59.00	111.75	102.50	88.63	70.08	10.56	9.56	9.23	7.68	17.75	14.63	36.38	34.46	38.41	32.13
54	LM47 x LM26	58.25	58.75	109.25	97.75	90.48	86.30	11.75	9.31	9.33	9.15	18.25	18.00	41.11	34.63	49.50	30.85
55	BW140 x BW141	53.00	56.25	106.00	101.75	74.90	61.03	10.31	10.81	6.88	7.00	14.38	13.50	30.71	29.75	45.38	36.47
56	BW152 x LM48	66.75	61.00	107.50	97.50	91.00	81.90	9.69	9.13	8.95	8.75	19.25	17.75	50.33	38.63	33.56	29.56
57	BW140	63.67	57.00	118.00	99.00	79.20	78.55	9.81	11.44	8.93	8.64	18.25	18.75	48.92	38.13	34.96	28.95
58	LM70 x LM71	62.25	61.00	108.25	92.25	81.88	89.70	11.31	10.31	11.88	10.19	22.63	19.00	45.06	35.08	41.67	29.27
59	LM26 x LM47	59.25	56.00	107.25	97.75	93.15	85.23	12.94	7.00	10.43	8.68	18.88	16.63	42.63	31.46	42.87	36.44
60	BW162 x BW152	60.00	62.50	100.25	97.75	90.60	80.48	11.00	9.81	9.56	9.50	18.13	18.13	37.92	31.04	41.82	32.61

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

No.	Genotype	DTH		DTM		PH		TN		SL		SPS		KPS		TKW	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
61	LM71 x BW152	62.67	62.25	108.00	96.50	76.78	76.75	7.06	11.63	7.88	7.78	14.75	15.50	29.75	28.92	42.76	33.02
62	LM48 x LM47	64.25	60.50	104.50	96.50	96.33	75.65	11.38	12.56	10.00	8.69	18.13	15.50	36.83	28.38	40.00	36.33
63	BW140 x LM26	56.75	56.00	110.75	101.75	85.83	78.45	13.00	5.36	8.48	7.81	18.00	15.63	35.54	28.88	34.79	36.18
64	LM47 x LM75	57.67	61.00	100.00	95.75	87.90	82.05	11.33	8.75	9.00	8.91	17.17	16.38	33.56	26.08	47.41	34.13
65	LM26 x LM70	56.75	57.00	105.00	98.75	92.78	82.68	9.63	9.00	10.53	9.54	19.44	17.50	35.89	34.67	39.96	32.78
66	LM71 x LM70	62.00	58.25	104.00	95.75	74.63	78.40	6.75	7.69	8.30	9.00	14.00	16.13	28.54	25.83	46.39	36.87
67	LM48 x LM75	60.75	61.00	102.50	96.75	89.35	69.80	9.44	6.38	9.50	7.70	19.00	14.38	46.50	32.88	36.79	33.69
68	LM48 x LM70	61.50	63.25	104.00	96.25	88.75	85.33	7.75	10.38	9.73	9.00	17.50	17.38	39.50	37.21	43.72	30.69
69	LM48 x BW152	62.25	60.75	102.75	96.50	83.80	87.43	10.50	7.55	9.18	8.70	15.75	15.75	39.88	29.21	38.67	32.42
70	BW140 x LM47	61.00	60.25	108.75	97.25	91.88	79.45	13.75	9.81	8.65	8.20	15.38	16.25	32.96	26.88	41.38	34.61
71	LM71 x BW141	57.50	56.25	110.50	100.50	74.00	77.18	7.06	11.60	8.50	7.75	15.88	15.38	36.08	30.50	33.88	36.31
72	BW141 x LM71	56.75	54.75	107.00	96.75	84.18	65.05	7.81	9.13	8.53	6.70	17.13	13.25	31.04	26.83	41.82	35.33
73	LM70	64.00	62.25	105.00	95.50	91.08	84.98	11.06	9.81	10.25	9.74	18.75	18.38	44.21	36.25	43.99	32.07
74	BW152 x BW140	58.75	54.75	112.00	98.00	86.08	74.33	9.25	9.81	8.68	7.60	19.63	15.83	46.38	20.39	38.87	28.88
75	BW152 x BW162	63.33	64.00	105.25	96.75	80.85	73.40	6.63	8.00	7.98	7.95	16.38	17.38	38.17	28.13	38.56	32.80
76	LM26 x BW152	60.00	62.33	107.00	101.00	91.10	80.73	12.31	8.75	9.87	8.73	20.00	17.25	48.54	30.29	37.27	37.82
77	BW141 x LM48	55.00	61.00	104.00	104.33	84.13	72.60	15.69	7.50	8.08	7.53	15.88	14.88	41.50	32.44	39.37	44.97
78	LM70 x LM48	70.00	66.00	112.50	112.00	93.90	91.30	8.25	4.25	10.60	9.30	20.00	18.00	53.67	23.67	37.50	50.00
79	LM47 x BW141	56.00	56.00	102.75	99.25	98.75	79.88	11.13	8.94	8.51	8.81	16.38	18.13	37.00	27.75	43.16	33.01
80	LM71 x LM47	61.50	63.25	103.25	96.25	88.93	83.43	10.50	7.46	10.93	9.35	18.63	16.50	45.88	33.75	43.48	36.21
81	BW141 x LM47	58.25	61.25	108.00	97.00	98.40	71.38	11.44	4.63	9.73	8.03	18.38	14.38	33.00	28.63	43.22	37.56
82	BW162 x LM70	64.67	61.50	104.00	96.75	72.35	82.08	8.00	9.81	8.56	9.58	15.38	17.00	25.00	31.79	50.00	38.58
83	BW162 x LM47	64.50	60.50	107.00	96.25	84.50	81.45	12.94	9.25	7.63	8.03	14.63	15.25	35.42	28.17	39.60	34.66
84	BW152 x LM71	59.50	61.75	103.25	96.50	83.95	83.50	5.19	9.88	7.98	9.24	15.00	17.13	31.58	34.71	45.34	30.91
85	LM71 x BW162	63.00	61.00	105.00	97.00	88.75	78.70	14.06	9.56	9.20	9.40	18.13	16.25	35.75	29.75	39.93	32.92
86	BW152 x LM47	63.75	64.75	106.50	95.75	89.73	77.03	8.50	8.06	9.20	7.75	18.50	15.88	41.38	29.79	39.60	32.47
87	LM48 x LM71	64.25	61.00	109.25	98.00	89.50	79.65	10.81	10.81	10.29	8.60	19.38	16.50	56.13	33.67	37.01	28.32
88	LM75 x LM26	56.25	58.25	105.25	99.75	89.48	74.53	10.81	7.88	9.41	7.83	18.88	16.25	42.08	29.13	43.44	28.29
89	BW141 x BW162	56.75	56.25	102.50	98.25	85.73	69.03	9.38	12.31	9.75	7.85	18.38	15.00	40.63	26.83	43.12	31.56
90	LM71	62.00	61.75	105.50	94.75	73.38	77.50	10.17	7.31	9.75	8.20	17.25	15.13	27.00	27.00	34.88	33.81

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

No.	Genotype	DTH		DTM		PH		TN		SL		SPS		KPS		TKW	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
<b>91</b>	LM48	63.00	62.00	104.00	96.00	82.40	67.25	7.88	7.13	8.00	7.60	15.25	13.88	38.63	30.00	31.09	26.75
<b>92</b>	BW141 x BW140	53.00	55.50	102.00	100.50	77.60	66.63	7.34	7.25	7.95	7.38	16.38	14.50	30.63	22.46	42.24	37.88
<b>93</b>	BW152 x LM70	60.50	61.25	99.50	94.00	94.23	85.00	10.25	12.06	9.99	9.25	18.13	17.13	40.46	25.21	43.14	30.54
<b>94</b>	LM47 x BW162	62.50	64.50	103.75	98.25	87.35	83.18	9.88	9.00	8.50	8.81	16.38	17.63	37.21	28.38	43.33	32.95
<b>95</b>	LM71 x LM48	58.25	64.50	105.75	97.75	92.48	87.98	13.56	9.00	9.89	9.50	19.13	18.13	39.79	38.29	37.62	29.97
<b>96</b>	BW162 x LM71	61.50	59.00	102.75	98.50	90.45	68.78	14.19	6.69	9.90	7.25	18.38	13.25	38.25	25.42	47.92	38.09
<b>97</b>	LM47 x LM71	63.25	63.00	103.75	94.75	93.55	76.50	9.38	7.63	9.50	8.10	18.38	14.63	37.42	29.75	42.37	27.64
<b>98</b>	LM47	64.50	65.25	106.25	98.00	90.13	71.33	10.13	6.63	9.73	8.49	17.25	15.63	34.33	24.42	45.13	38.10
<b>99</b>	LM75 x LM71	59.50	62.00	106.25	95.50	84.53	84.05	12.63	10.50	9.80	8.92	18.75	19.17	43.92	33.06	37.14	24.17
<b>100</b>	BW152	61.50	63.00	103.00	96.25	88.65	60.45	14.68	7.19	9.20	6.95	16.38	15.38	31.46	26.04	42.78	33.62
	<b>Mean</b>	59.90	59.44	105.90	98.17	87.27	79.76	10.47	9.42	9.14	8.58	17.53	16.51	38.69	32.45	40.89	33.82
	<b>LSD</b>	4.14	4.56	6.13	5.63	13.64	13.49	4.99	5.85	1.22	1.78	2.34	3.46	12.25	11.27	7.00	6.94
	<b>SEM</b>	0.35	0.29	0.31	0.30	0.64	0.71	0.23	0.21	0.09	0.08	0.17	0.14	0.58	0.48	0.37	0.39
	<b>CV</b>	5.90	4.85	2.93	3.04	7.27	8.85	21.66	21.79	9.78	9.46	9.52	8.69	14.96	14.71	9.10	11.39

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), LSD = least significant difference, SEM = standard error of mean, %CV = coefficient of variation, NS = non-stressed, DS = drought-stressed

## Appendix 3.1 continued

No.	Genotype	SB		RB		PB		RS		GY	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
1	LM75	239.58	297.30	49.96	70.25	682.40	680.32	0.29	0.26	335.78	267.32
2	LM26 x BW140	233.25	199.69	27.20	54.92	572.95	536.96	0.17	0.29	267.10	241.33
3	BW140 x LM71	170.75	177.42	13.00	32.88	443.28	458.36	0.07	0.18	221.82	215.63
4	LM47 x BW152	191.85	301.13	13.29	53.94	417.31	594.91	0.06	0.18	209.51	204.99
5	LM70 x BW152	308.13	201.93	15.19	40.57	733.45	479.53	0.06	0.25	350.53	202.60
6	LM70 x BW141	158.63	188.03	27.72	30.77	584.77	448.72	0.41	0.15	340.52	196.52
7	BW162 x LM75	289.19	252.30	37.16	64.09	764.35	537.48	0.10	0.25	436.16	188.96
8	LM75 x BW141	231.36	212.91	33.32	28.82	669.32	457.69	0.15	0.12	345.85	184.58
9	BW152 x BW141	147.57	265.18	28.12	65.07	514.11	542.62	0.19	0.33	255.81	181.52
10	LM70 x BW162	214.65	173.67	26.08	53.36	468.07	438.48	0.21	0.38	223.02	180.73
11	BW141 x LM26	338.36	174.62	42.10	28.91	657.34	289.35	0.14	0.22	313.93	178.91
12	LM48 x BW140	369.12	155.91	48.37	32.60	962.54	396.74	0.11	0.21	465.86	177.98
13	LM75 x LM47	228.06	288.63	28.09	37.59	612.34	519.75	0.13	0.15	304.43	177.73
14	LM70 x LM26	197.57	242.52	15.81	54.35	441.47	515.55	0.08	0.28	194.95	172.00
15	LM47 x BW140	211.62	216.17	24.29	54.99	582.29	486.55	0.12	0.26	296.05	171.01
16	LM26 x LM71	306.70	231.70	41.22	45.08	640.76	476.35	0.14	0.21	290.47	170.58
17	BW141 x LM75	304.99	207.99	19.75	49.06	607.51	455.56	0.08	0.23	285.74	169.67
18	BW162 x LM26	240.26	243.97	38.05	54.59	544.58	427.52	0.16	0.22	227.57	166.10
19	LM26 x BW141	217.49	147.15	37.95	21.70	662.21	362.72	0.21	0.15	347.67	165.70
20	LM71 x LM26	388.93	199.61	41.80	50.42	1013.32	443.01	0.16	0.27	497.95	164.94
21	BW152 x LM75	302.57	211.06	44.54	32.87	836.91	435.93	0.13	0.20	418.63	164.10
22	LM48 x BW162	284.74	154.69	11.01	44.14	590.89	404.77	0.06	0.40	305.60	164.01
23	LM75 x BW152	264.24	200.45	31.95	41.28	768.67	396.66	0.13	0.22	403.83	163.14
24	BW152 x LM26	194.58	126.02	23.09	30.36	473.93	346.79	0.14	0.29	219.02	162.75
25	BW140 x LM75	327.32	174.01	68.54	30.95	851.62	391.42	0.23	0.16	394.29	159.36
26	BW140 x BW152	298.51	203.99	28.78	63.06	501.67	402.42	0.13	0.27	265.31	159.29
27	BW162 x BW140	168.03	170.87	16.06	57.73	479.04	417.75	0.10	0.30	252.10	158.99
28	LM75 x BW140	262.87	186.13	30.43	47.17	685.52	419.07	0.14	0.23	335.23	158.77
29	LM71 x BW140	329.99	204.43	31.23	28.99	699.22	418.77	0.12	0.17	295.56	158.42
30	BW141 x LM70	375.67	359.04	22.18	25.14	822.03	569.22	0.08	0.11	362.55	158.15

SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>), NS = non-stressed, DS = drought-stressed

## Appendix 3.1 continued

No.	Genotype	SB		RB		PB		RS		GY	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
31	LM75 x LM48	248.28	227.76	24.20	52.55	541.43	464.02	0.12	0.29	282.93	157.01
32	BW141 x BW152	354.91	175.07	38.04	34.05	737.05	392.32	0.13	0.22	294.10	156.58
33	LM75 x LM70	228.70	172.53	28.18	17.56	528.53	371.14	0.14	0.09	232.17	154.74
34	LM70 x LM47	275.18	286.85	28.72	36.80	842.77	484.41	0.09	0.14	374.15	154.45
35	LM26 x LM48	234.84	133.14	29.92	32.37	692.11	345.19	0.14	0.27	365.26	153.57
36	BW162	307.79	124.96	26.75	28.12	771.99	331.71	0.12	0.28	373.88	152.67
37	BW140 x LM70	228.48	143.97	28.62	47.66	540.94	369.63	0.13	0.65	242.60	152.14
38	LM70 x LM75	371.09	265.52	47.30	29.55	947.47	472.59	0.13	0.10	452.21	151.73
39	LM47 x LM70	181.44	246.43	24.38	38.46	412.26	461.89	0.14	0.16	176.44	151.28
40	LM47 x LM48	248.33	251.02	25.92	27.09	586.48	480.80	0.12	0.12	266.87	151.00
41	LM26 x BW162	264.61	272.42	34.58	50.50	737.26	498.24	0.14	0.19	374.41	149.85
42	LM48 x LM26	223.14	231.05	26.10	49.37	673.73	454.77	0.12	0.22	362.82	149.02
43	BW162 x LM48	270.60	218.48	34.92	56.46	647.42	446.25	0.13	0.29	292.22	146.42
44	BW141	167.72	164.62	15.23	23.32	411.06	358.36	0.10	0.16	194.97	145.66
45	LM75 x BW162	300.98	176.51	33.09	30.00	701.57	375.95	0.11	0.19	314.11	144.82
46	BW140 x BW162	244.74	115.98	38.52	16.51	667.47	299.28	0.19	0.20	328.38	142.56
47	LM71 x LM75	413.78	184.35	43.39	38.42	1019.04	389.43	0.16	0.27	480.24	142.45
48	LM70 x BW140	156.74	149.50	45.10	17.02	435.10	332.62	0.66	0.13	197.30	141.96
49	LM26 x LM75	350.90	211.09	40.12	53.31	954.03	429.96	0.15	0.28	481.21	141.50
50	BW162 x BW141	266.05	180.52	75.71	43.27	776.54	386.17	0.26	0.23	371.60	138.78
51	BW140 x LM48	112.54	125.04	7.14	23.04	278.22	308.84	0.07	0.22	151.68	137.40
52	LM26	291.13	122.65	17.21	28.51	674.12	276.83	0.07	0.60	312.63	137.19
53	LM48 x BW141	287.87	156.44	39.73	24.30	602.09	340.23	0.20	0.21	234.61	136.32
54	LM47 x LM26	282.00	192.87	51.35	28.92	804.19	380.20	0.17	0.16	449.20	135.81
55	BW140 x BW141	167.00	121.89	20.39	20.09	460.77	300.00	0.11	0.24	238.01	135.06
56	BW152 x LM48	267.76	178.29	22.87	38.54	692.08	374.66	0.09	0.16	343.12	134.90
57	BW140	281.02	169.50	27.62	42.47	656.31	365.69	0.09	0.27	353.33	131.38
58	LM70 x LM71	186.01	289.16	22.67	64.86	522.58	507.64	0.18	0.24	266.99	131.30
59	LM26 x LM47	322.08	166.32	37.34	36.65	768.22	356.54	0.12	0.28	349.40	131.25
60	BW162 x BW152	242.65	244.84	53.62	32.65	644.57	455.70	0.23	0.21	297.69	130.49

SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>), NS = non-stressed, DS = drought-stressed

## Appendix 3.1 continued

No.	Genotype	SB		RB		PB		RS		GY	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
61	LM71 x BW152	225.04	163.97	21.24	34.45	604.82	359.81	0.12	0.22	227.61	130.41
62	LM48 x LM47	299.65	120.72	26.80	30.80	552.61	303.67	0.10	0.34	235.58	130.04
63	BW140 x LM26	283.59	150.38	31.09	24.11	670.11	325.65	0.11	0.19	303.78	129.20
64	LM47 x LM75	254.44	212.38	33.94	31.35	634.92	393.28	0.13	0.16	296.19	127.82
65	LM26 x LM70	369.95	197.27	31.99	17.41	625.15	395.97	0.08	0.20	258.98	127.72
66	LM71 x LM70	138.22	146.78	18.28	41.87	411.76	337.39	0.15	0.26	233.06	127.13
67	LM48 x LM75	275.22	123.82	25.69	21.65	765.71	237.56	0.14	0.24	397.27	125.23
68	LM48 x LM70	337.22	181.24	18.41	59.07	800.17	385.80	0.08	0.30	379.95	124.35
69	LM48 x BW152	174.58	200.71	50.77	28.29	546.33	346.80	0.25	0.23	274.34	124.07
70	BW140 x LM47	184.46	230.98	46.98	69.38	556.07	444.20	0.46	0.29	277.45	122.94
71	LM71 x BW141	162.61	160.60	23.11	45.84	478.25	349.70	0.27	0.26	250.02	122.44
72	BW141 x LM71	173.86	96.06	20.55	18.39	427.39	231.54	0.13	0.14	199.13	119.20
73	LM70	365.06	245.33	19.11	42.40	847.96	426.63	0.07	0.17	396.39	118.71
74	BW152 x BW140	288.63	160.45	23.31	53.34	730.11	393.69	0.08	0.31	357.41	118.60
75	BW152 x BW162	170.07	131.74	18.00	17.57	450.42	272.57	0.10	0.22	224.23	117.65
76	LM26 x BW152	348.96	157.93	44.96	27.50	910.06	322.86	0.21	0.17	441.14	117.46
77	BW141 x LM48	229.43	119.85	23.30	18.31	683.91	280.77	0.11	0.25	356.58	117.25
78	LM70 x LM48	180.83	128.33	10.03	12.15	516.84	287.19	0.10	0.17	271.77	116.67
79	LM47 x BW141	253.48	179.62	31.28	73.29	595.31	387.78	0.12	0.44	265.43	115.28
80	LM71 x LM47	244.24	167.27	26.54	28.76	545.48	284.85	0.13	0.37	276.88	115.09
81	BW141 x LM47	236.86	104.70	32.00	25.11	598.02	262.04	0.18	0.41	281.34	113.02
82	BW162 x LM70	102.23	98.74	13.59	39.68	270.87	265.10	0.13	0.42	176.69	112.73
83	BW162 x LM47	226.81	205.60	33.90	39.29	595.36	374.49	0.21	0.19	292.67	110.77
84	BW152 x LM71	151.59	189.16	42.60	44.03	562.41	357.08	0.24	0.20	226.02	105.89
85	LM71 x BW162	374.76	162.53	31.60	30.87	830.54	296.63	0.09	0.30	362.54	104.44
86	BW152 x LM47	269.27	148.63	23.75	36.37	585.16	306.76	0.09	0.25	249.69	104.06
87	LM48 x LM71	326.32	221.77	36.43	82.97	897.12	424.90	0.19	0.38	456.72	102.69
88	LM75 x LM26	274.35	102.73	26.17	30.51	764.08	252.22	0.10	0.33	396.20	101.69
89	BW141 x BW162	186.70	153.22	25.53	33.58	525.70	304.95	0.17	0.24	267.93	100.99
90	LM71	216.93	130.79	36.02	28.57	593.20	277.39	0.14	0.20	241.39	100.87

SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>), NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

No.	Genotype	SB		RB		PB		RS		GY	
		NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
<b>91</b>	LM48	153.67	106.63	13.73	21.78	434.85	208.83	0.10	0.41	228.59	100.27
<b>92</b>	BW141 x BW140	165.03	125.72	24.59	27.37	462.64	270.09	0.15	0.34	233.34	100.01
<b>93</b>	BW152 x LM70	267.00	272.00	54.38	28.83	672.66	360.14	0.19	0.11	300.24	99.55
<b>94</b>	LM47 x BW162	204.81	176.25	41.11	36.82	510.12	329.31	0.23	0.21	225.81	99.36
<b>95</b>	LM71 x LM48	321.24	196.36	58.69	40.68	824.41	353.02	0.18	0.32	379.90	99.13
<b>96</b>	BW162 x LM71	334.12	103.75	25.92	14.65	809.10	225.54	0.09	0.18	432.71	91.57
<b>97</b>	LM47 x LM71	277.87	196.21	27.94	31.15	715.38	283.55	0.12	0.20	350.05	89.96
<b>98</b>	LM47	271.05	151.17	22.85	32.64	657.22	287.85	0.08	0.20	310.53	88.92
<b>99</b>	LM75 x LM71	323.36	347.87	46.38	73.42	763.69	505.65	0.15	0.21	336.71	72.11
<b>100</b>	BW152	399.15	121.55	31.00	23.24	922.43	199.76	0.09	0.32	420.74	67.00
	<b>Mean</b>	256.20	186.60	30.99	38.06	643.60	384.80	0.15	0.24	310.10	141.20
	<b>LSD</b>	141.90	142.30	31.26	33.76	342.70	250.60	0.23	0.23	183.10	95.90
	<b>SEM</b>	6.97	5.52	1.24	1.51	15.71	9.04	0.01	0.01	7.87	3.37
	<b>CV</b>	27.21	29.59	40.07	39.55	24.41	23.50	56.06	38.27	25.37	23.87

SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ), RS = root to shoot ratio and GY = grain yield ( $\text{g m}^{-2}$ ), LSD = least significant difference, SEM = standard error of mean, %CV = coefficient of variation, NS = non-stressed, DS = drought-stressed

Appendix 3.2. Direct (bold face values) and indirect effects for yield components and root attributes on grain yield of 10 bread wheat parental lines and 90 F<sub>2</sub> progenies under drought-stressed conditions at two sites.

Traits	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	SB	RB	PB	RS	GY
<b>DTH</b>	<b>-0.19</b>	0.06	-0.05	0.01	-0.05	-0.02	0.01	0.03	-0.03	-0.01	0.01	-0.01	-0.38***
<b>DTM</b>	-0.02	<b>0.06</b>	-0.02	-0.01	-0.02	-0.01	0.00	0.02	-0.01	0.00	0.00	0.01	0.24*
<b>PH</b>	0.01	-0.01	<b>0.03</b>	0.01	0.03	0.02	0.01	-0.01	0.02	0.01	0.02	-0.01	0.26**
<b>TN</b>	0.00	0.00	0.01	<b>0.03</b>	0.01	0.01	0.01	-0.01	0.02	0.02	0.02	0.00	0.34***
<b>SL</b>	0.00	0.00	0.00	0.00	<b>0.00</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24*
<b>SPS</b>	-0.02	0.02	-0.08	-0.04	-0.10	<b>-0.13</b>	-0.07	0.05	-0.07	-0.05	-0.07	0.02	0.26*
<b>KPS</b>	-0.01	-0.02	0.13	0.08	0.17	0.18	<b>0.34</b>	-0.10	0.14	0.08	0.17	-0.04	0.55***
<b>TKW</b>	-0.02	0.06	-0.03	-0.04	-0.04	-0.06	-0.05	<b>0.16</b>	-0.07	-0.06	-0.04	-0.01	0.09
<b>SB</b>	-0.06	0.09	-0.29	-0.22	-0.26	-0.24	-0.17	0.16	<b>-0.41</b>	-0.24	-0.36	0.13	0.39***
<b>RB</b>	-0.01	0.01	-0.06	-0.08	-0.06	-0.06	-0.04	0.05	-0.09	<b>-0.15</b>	-0.10	-0.06	0.28**
<b>PB</b>	-0.06	-0.03	0.60	0.57	0.54	0.55	0.50	-0.26	0.88	0.65	<b>1.00</b>	-0.19	0.68***
<b>RS</b>	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.00	-0.01	0.01	-0.01	<b>0.03</b>	-0.14

\* significant at P < 0.05; \*\* P < 0.01, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>).

Appendix 3.3. Direct (bold face values) and indirect effects for yield components and root attributes on grain yield of 10 bread wheat parental lines and 90 F<sub>2</sub> progenies under non-stressed conditions at two sites.

Traits	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	SB	RB	PB	RS	GY
<b>DTH</b>	<b>-0.02</b>	0.00	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
<b>DTM</b>	0.00	<b>0.03</b>	0.00	0.00	0.00	0.01	0.00	-0.01	0.00	0.00	0.00	0.00	0.02
<b>PH</b>	0.00	0.00	<b>0.00</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.48***
<b>TN</b>	0.00	0.00	0.03	<b>0.08</b>	0.02	0.02	0.01	0.00	0.05	0.03	0.05	0.00	0.60***
<b>SL</b>	0.00	0.00	0.00	0.00	<b>-0.01</b>	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.41***
<b>SPS</b>	0.00	0.00	0.01	0.00	0.01	<b>0.01</b>	0.01	0.00	0.01	0.00	0.01	0.00	0.48***
<b>KPS</b>	0.02	0.01	0.04	0.02	0.06	0.08	<b>0.13</b>	-0.03	0.04	0.01	0.05	-0.02	0.48***
<b>TKW</b>	0.00	-0.02	0.02	0.00	0.01	0.00	-0.02	<b>0.08</b>	0.00	0.01	0.01	0.01	0.13
<b>SB</b>	-0.02	-0.02	-0.10	-0.11	-0.09	-0.09	-0.06	-0.01	<b>-0.19</b>	-0.07	-0.16	0.05	0.73***
<b>RB</b>	0.02	0.00	-0.04	-0.06	-0.03	-0.03	-0.01	-0.01	-0.05	<b>-0.13</b>	-0.07	-0.09	0.41***
<b>PB</b>	0.04	0.03	0.55	0.66	0.44	0.50	0.43	0.11	0.89	0.52	<b>1.06</b>	-0.05	0.94***
<b>RS</b>	-0.01	0.00	0.00	0.00	0.00	-0.01	-0.01	0.01	-0.02	0.04	0.00	<b>0.07</b>	-0.03

\* significant at P < 0.05; \*\* P < 0.01, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tiller number, SL = spike length (cm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>), RS = root to shoot ratio and GY = grain yield (g m<sup>-2</sup>).

## **Chapter 4: Genetic Analysis of Yield and Yield-related Traits and Biomass Allocation in Newly Developed Wheat (*Triticum aestivum* L.) Populations**

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### **Abstract**

Root biomass is a major soil-organic carbon source and may confer drought adaptation in water-limited environments. Understanding the genetic bases and inheritance of yield-related traits and biomass allocation is fundamental for drought tolerance breeding and soil health. The objective of this study was to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat to identify good combiners for breeding and enhanced carbon sequestration. Ten selected wheat genotypes were crossed in a full diallel mating design, and 90 F<sub>2</sub> families were generated and evaluated in the field and greenhouse under drought-stressed and non-stressed conditions. Significant differences were recorded among the tested families revealing substantial variation for plant height (PH), kernels per spike (KPS), root biomass (RB), shoot biomass (SB), total plant biomass (PB) and grain yield (GY). Additive gene effects conditioned PH, SB, PB and GY under drought, suggesting the polygenic inheritance for drought tolerance. Strong maternal and reciprocal genetic effects were recorded for RB across the testing sites under drought-stressed conditions. The parental line LM75 maintained the general combining ability (GCA) effects in a positive and desirable direction for SB, PB and GY. Early generation selection using PH, SB, PB and GY will improve drought tolerance by exploiting additive gene action under drought conditions. Higher RB production may be maintained by a positive selection of male and female parents to capture the significant maternal and reciprocal effects found in this study.

**Keywords:** *Carbon sequestration, Drought, Gene action, Maternal effects, Root biomass, Wheat*

## 4.1 Introduction

Bread wheat (*Triticum aestivum* L.,  $2n=6x=42$ , AABBDD) is an important grain crop contributing to 40% of the calorie intake of the global population (Upadhyay, 2020; Grote et al., 2021). Because of decreases in the frequency and amount of precipitation, drought-induced yield losses are projected to increase annually at a rate of 3% for wheat, thereby necessitating the development of drought-tolerant cultivars adapted to semi-arid regions (Gupta et al., 2020; Brás et al., 2021). Root system traits (e.g. root biomass, root angle, root length, root length density and root surface area) are ideal attributes that can be exploited in breeding programs to increase water use efficiency and crop productivity under drought conditions (Comas et al., 2013; Janiak et al., 2016; Siddiqui et al., 2021). High root biomass is important to capture moisture from light rain showers or irrigation and access deeper water in the soil profile under terminal drought conditions (Becker et al., 2016). In a study comparing root system plasticity among near-isogenic lines, Ehdaie et al. (2012) reported higher yield potential in lines that produced more root biomass than lines that had less root biomass. Wild relatives and primitive genotypes of wheat develop more root biomass associated with drought avoidance and better yield potential under severe drought than cultivated wheat (Li et al., 2021). Thus, increasing plant biomass allocation to the roots of modern wheat cultivars will be crucial for adaptation to dry environments and yield gains.

Environmental stresses cause plants to change biomass allocation patterns for adaptation, survival, and reproduction (Dolezal et al., 2021). Based on the optimal partitioning theory (OPT), crop plants, including wheat, will allocate more biomass to the roots system under moisture stress (Kobe et al., 2010). Notably, different allelic combinations cause intraspecific variation in wheat biomass allocation resulting in different genotype responses to drought stress (Edwards et al., 2016; Mathew et al., 2019). Hence, promising genotypes can be identified and used in crossing programs to develop breeding populations to select transgressive segregants with high root biomass and carbon sequestration potential (McCarthy and Enquist, 2007; Mathew et al., 2019). Nevertheless, focusing on biomass allocation alone without maximizing yield-related traits may lead to a loss of wheat productivity. In wheat breeding, plant height, kernels per spike and harvest index are key yield-related traits that have been targeted for drought tolerance breeding (Rivera-Amado et al., 2019; Shamyarira et al., 2022). Multiple traits selection for high biomass production and grain yield-related attributes may be required to increase genetic gains in wheat breeding programs (Reynolds et al., 2017)

Breeding gains have been achieved by understanding the genetic basis and inheritance of yield components and creating desirable progenies through combining ability (CA) analysis (Aycañ et al., 2021). The goals of CA analysis are to identify genetically superior lines with high breeding values and to identify desirable cross combinations to improve average performances for cultivar development (Rukundo et al., 2017; Yadav et al., 2021). Combining ability analysis can be done at F<sub>2</sub> generation without substantial loss of information on the breeding values of parental lines (Bhullar et al., 1979). Several studies have conducted genetic analysis on F<sub>2</sub> populations in self-pollinating crops such as wheat (Mwadingeni et al., 2018; Rembe et al., 2019), soybean (Ibanda et al., 2018; Teodoro et al., 2019), common bean (Nkhata et al., 2021) and groundnut (Daudi et al., 2021).

Estimates of combining ability effects and the extent of variance components reveal the magnitude of both additive and non-additive gene action (Fasahat et al., 2016; Mohammadi et al., 2021). In hybrid breeding, additive, dominance and epistatic interactions of non-allelic genes influence maximum heterosis (Whitford et al., 2013). On the other hand, additive gene effects are more important in line breeding with minimal contribution from non-additive gene effects, which are lost during segregation in early generations (Adhikari et al., 2019). As a result, maternal effects (inheritance of cytoplasmic genes from mitochondria and chloroplasts and their interaction with nuclear genes), are often ignored in explaining variation among genotypes (Roach and Wulff, 1987; Yildirim et al., 2008). In pure line cultivar development, maternal effects can be exploited to identify male and female lines in crosses to maximise genetic gain for traits with significant reciprocal effects (Mahgoub 2011).

Diallel analysis can aid in partitioning the general combining ability (GCA) and specific combining ability (SCA) effects. It also reveals the magnitude of maternal effect that will be useful in breeding of wheat. Maternal effects contribute to early seedling development and biomass production of plants (Iida et al., 2013). Understanding the magnitude of variation attributed to cytoplasmic DNA would greatly enhance selection efficiency, including in root biomass. Several studies have reported significant maternal effects in crops for agronomic traits. Singh et al. (2017) pointed out a maternal effect influencing root traits in F<sub>1</sub> reciprocal crosses in common bean (*Phaseolus vulgaris* L.). Additionally, Aycañ et al. (2021) reported that salt stress tolerance levels in reciprocal crosses of wheat were related to the maternal plants of the respective progenies. In a study to

improve pre-harvest sprouting in barley, Nakamura et al. (2017), reported that seed dormancy was maternally inherited. Conversely, no significant maternal effects have been reported for wheat grain yield, though small numbers of crosses reflected significant reciprocal effects (Easterly et al., 2020). Based on the reports mentioned above, there may be significant maternal and reciprocal effects for root biomass allocation and other traits of interest in wheat.

Biomass allocation is an important attribute in developing drought-tolerant crop ideotypes that contribute to yield gains and carbon sequestration. To our knowledge, there is not enough information on genetic analysis of biomass allocation for trait integration and to guide selection and breeding in wheat. To examine the pattern of genetic inheritance of biomass allocation, 10 selected bread wheat lines with contrasting root biomass and drought tolerance were crossed using a full-diallel mating design, and the developed crosses were advanced to the F<sub>2</sub> generation. Therefore, the objectives of this study were to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat; and to identify good combiners for breeding and enhanced carbon sequestration. Information from this study will help determine the suitable parental selection criteria for the efficient breeding of climate-smart wheat cultivars.

## **4.2 Materials and methods**

### **4.2.1 Plant material, crosses and genetic advancement**

Ten genotypes were selected based on their genetic diversity, drought tolerance and ability to produce shoot and root biomass under drought conditions. The pedigree information and the drought sensitivity index (DSI) of the genotypes is summarized on Table 3.1. Eight of the lines were drought and heat tolerant lines acquired from the CIMMYT drought, and heat nurseries and two lines were local checks with good drought resistance. Crossing blocks of the ten genotypes were established from April to June 2019 at the Controlled Environment Facilities (CEF) at the University of KwaZulu-Natal, South Africa. The parental lines were stagger planted to allow synchronized flowering for emasculation and pollination. A total of 90 families were developed, including 45 direct crosses and 45 reciprocals using a full-diallel mating design. Successful F<sub>1</sub> crosses were harvested from August to October 2019 and bulked to produce F<sub>2</sub> seed in a multiplication trial from December 2019 to March 2020.

## **4.2.2 Phenotypic evaluation**

### **4.2.2.1 Field evaluation**

One hundred genotypes including 10 parents and 90 F<sub>2</sub> families were planted at the Ukulinga Research Farm (29° 40' S, 30° 24' E; 806 m above sea level) in a field trial in July 2020. The trial was laid out in a 10 × 10 alpha lattice design with two replications. Test plots were 1m long, with five planting stations spaced 20 cm apart. Three seeds were planted per planting station and were later thinned to two plants two weeks after germination. Outer field rows were planted with a local cultivar to reduce border effects. An automated drip irrigation system was used to provide water and fertilizer equally to all plants. The trials were conducted under two water regimes: drought-stressed and non-stressed. Drought-stress was imposed by allowing depletion of water in the rooting zone to 35% field capacity at the heading stage of growth in the drought-stressed treatment. In the non-stressed treatment, irrigation was continued by maintaining watering at 80% of field capacity until crop maturity. The amount of water in the soil was measured using a tensiometer reading (HOBO UX120, Onset, USA) located in each replication to a depth of 60cm of the rooting zone. Standard agronomic practices were kept constant in both water regimes for the duration of the trials according to wheat production guidelines in South Africa (DAFF 2016). Weather conditions at the site were recorded and reported (Shamuyarira et al., 2022).

### **4.2.2.2 Greenhouse evaluation**

The greenhouse experiment was conducted at the Controlled Environment Facilities at the University of KwaZulu-Natal (29° 37' S, 30° 24' E). The experiment was arranged in a 10 × 10 alpha lattice design, with two replications following the pattern of the field experiment. Seven seeds were sown in 10 L capacity plastic pots filled with 6 L of composited pine bark growing media. Germinated seedlings were thinned to five plants per pot. Fertigation was supplied to the rooting zone using an automated irrigation system to provide sufficient water and fertilizer to the plants. The experiments were carried out under two water regimes, namely: drought-stressed; and non-stressed conditions. At the heading stage, stress was imposed in the drought-stressed treatment by depleting water to 35% of field capacity. The non-stressed treatment continued to receive adequate watering to maintain pots at 80% of field capacity until crop maturity. A hand-held moisture probe was used to monitor soil moisture availability in the pots. Insecticides (pyridine azomethine) and fungicides (triazole) were used to control aphids and powdery mildew,

respectively. Day and night temperatures of 25 C and 15 C, respectively and humidity between 45% and 55% were maintained in the greenhouse for the duration of the trial.

### **4.2.3 Data collection**

The following morpho-agronomic traits were measured and recorded. Plant height (PH) was measured as the height of the plant from the soil to the tip of the spike using a calibrated meter rule in centimetres (cm). The number of kernels per spike (KPS) was recorded as the number of seeds manually counted from each individual spike, and shoot biomass (SB) was recorded as the above-ground biomass cut from the base of the plant, including stems and leaves but excluding grain. Root biomass (RB) was recorded as the total root dry matter harvested per genotype per plot. Root samples for each plot were harvested to a depth of 50 cm using a 30 × 30 × 30 cm monolith sampling box. Large roots were separated manually before washing under running water to remove soil particles. The remaining soil was mixed with water and the suspension was sieved through a 2 mm sieve to collect the fine roots. The fine roots collected from the sieve residue were added and weighed together with the large roots. The shoot and root samples were oven dried at 70°C for 48 h separately. Dry matter for SB and RB were weighed and expressed in g m<sup>-2</sup>. Total plant biomass (PB) was recorded as the total plant dry matter for each genotype in g m<sup>-2</sup>. It was calculated by summing up the weight for RB, SB and grain yield (GY) harvested for each genotype. Grain yield was recorded as the total harvested grain per genotype and weighed on a laboratory precision digital scale. The weight of the grain was adjusted to 12.5% moisture content and expressed in g m<sup>-2</sup>. Harvest index was calculated as the ratio of GY to total above-ground biomass including grain yield (GY/GY + SB).

### **4.2.4 Data analyses**

#### **4.2.4.1 Analysis of variance**

A separate analysis of variance (ANOVA) and Bartlett's test for homogeneity of variance for the two study sites showed significant differences for genotypes and water regimes with homogeneous and comparable variances. Therefore, a combined ANOVA was conducted across the two study sites for the 10 parents and 90 F<sub>2</sub> families using Genstat 18<sup>th</sup> Edition (Payne et al., 2017).

#### 4.2.4.2 Estimation of general and specific combining ability effects

Genetic analysis for a full diallel mating design was computed separately for each test environment using AGD-R Statistical Software (Rodriguez et al., 2015). The general combining ability (GCA) and specific combining ability (SCA) estimates were determined according to Griffing (1956) Diallel Method I, Model I, following the statistical formula below:

$$Y_{ij} = \mu + g_i + g_j + S_{ij} + r_{ij} + b_k + e_{ijk}$$

Where:  $Y_{ij}$  = phenotypic observation on a cross between the parents i and j,  $\mu$  = overall mean,  $g_i$  = GCA effect of parent i,  $g_j$  = GCA effect of parent j,  $S_{ij}$  = SCA effect of a cross between parent i and parent j,  $r_{ij}$  = reciprocal effect for the reciprocal crosses between the ith and jth parents,  $b_k$  = effect of the kth block,  $e_{ijk}$  = experimental error due to the environmental effect.

The relative GCA and SCA ratio was calculated to determine the gene action for each trait using the following formula according to Baker (1978):

$$\frac{GCA}{SCA} \text{ ratio} = \frac{2\sigma_{gca}^2}{(2\sigma_{gca}^2 + \sigma_{sca}^2)}$$

Where:  $\sigma_{gca}^2$  = variance due to GCA and  $\sigma_{sca}^2$  = variance due to SCA

The broad sense heritability of recorded traits was calculated using the formula below:

$$H^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

Where  $H^2$  = broad sense heritability,  $\sigma_g^2$  = genetic variance and  $\sigma_p^2$  = phenotypic variance

### 4.3 Results

#### 4.3.1 Analysis of variance

The combined analysis of variance with mean squares and significant tests for biomass traits and yield components is presented in Table 4.1. The effects of family and family  $\times$  site interaction were significant for plant height (PH), shoot biomass (SB), root biomass (RB), total plant biomass (PB) and grain yield (GY) but were not significant for harvest index (HI). The interaction of family and water regime was significant only for GY. No significant differences were observed for family  $\times$  water regime  $\times$  site interaction for all traits.

Table 4.1. Mean squares and significant tests from the combined analysis of variance of ten bread wheat parental lines, 45 direct crosses and 45 reciprocal crosses for yield components and biomass traits evaluated at two sites under drought-stressed and non-stressed conditions

<b>SOV</b>	<b>d f</b>	<b>PH</b>	<b>KPS</b>	<b>SB</b>	<b>RB</b>	<b>PB</b>	<b>GY</b>	<b>HI</b>
<b>Rep</b>	1	142.45	212.15	4484	10390.90***	220237.00*	43869.00*	0.15
<b>Block</b>	18	176.89*	115.63*	25982.00***	994.50*	67304	21502.00**	161.84**
<b>Family</b>	99	243.27***	142.25***	18128.00***	769.50**	69654.00***	14638.00**	80.21
<b>Water Regime (WR)</b>	1	11091.44***	7189.67***	938657.00***	10709.50***	12251041.00***	5465271.00***	16424.81***
<b>Site</b>	1	89648.69***	67179.66***	2054036.00***	24588.50***	1132252.00***	165356.00***	28620.09***
<b>Family.WR</b>	99	104.61	71.7	11642	631.9	53980	13481.00*	67.94
<b>Family.Site</b>	98	149.27***	94.62*	17491.00***	756.10*	67155.00**	14496.00*	72.92
<b>Family.WR.Site</b>	97	116.64	72.21	12166	577.7	45619	12154	75.58
<b>Residual</b>	368	91.79	66.81	10071	533	43026	10167	63.21

SOV = source of variation, d.f = degrees of freedom, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ )

### 4.3.2 Mean performance of parental lines and F<sub>2</sub> families

Drought stress substantially impacted all measured traits, with the mean PH reduced by 9.38 cm and 5.94 cm in the field and greenhouse, respectively (Tables 4.2 and 4.3). The percentage drop in KPS due to drought stress was 19.18% in the field which was double that of 8.8% in the greenhouse. Drought-stress positively impacted root growth, which increased by 78% in the greenhouse but had a reduced effect on RB in the field. Biomass traits were severely reduced by drought with SB experiencing losses of 41.09 gm<sup>-2</sup> and 100.82 gm<sup>-2</sup> while PB had losses of 181.40 gm<sup>-2</sup> and 327.39 gm<sup>-2</sup> in the field and greenhouse, respectively. Grain yield reductions due to drought stress were up to 120.67 gm<sup>-2</sup> in the field and 410.31 gm<sup>-2</sup> in the greenhouse. This represented a yield loss of 40.27% and 80.21% in the field and greenhouse, respectively. Plant height and KPS had higher mean values in the field than in the greenhouse under both water regimes. On the other hand, higher mean values were observed in the greenhouse than in the field for RB and PB under drought-stressed and non-stressed conditions.

Some parents and families were more drought tolerant than others. For instance, parental lines LM75 and BW162 had the highest grain yield and biomass production than the other parents under drought-stressed conditions. Kernels per spike were high in lines LM26 and LM75 under the same conditions. The highest yielding parents under non-stressed conditions were BW140 (with a grain yield of 398.70 gm<sup>-2</sup>) and BW162 (355.67 gm<sup>-2</sup>) in the field, while BW152 (597.07 gm<sup>-2</sup>) and LM70 (505.65 gm<sup>-2</sup>) yielded better in the greenhouse conditions. The same genotypes scored high for SB, RB and PB. The tallest genotypes under non-stressed conditions were LM47 and LM70 in the field and greenhouse, respectively. Several families outperformed the parents for RB (e.g. BW141 × LM26), PB (LM47 × BW152) and GY (LM26 × BW140) under drought-stressed conditions. Similar trends were observed under non-stressed conditions. The mean harvest index under drought stressed conditions was 48.52% and 34.03% in the field and greenhouse respectively. Under non-stressed conditions the mean HI was 55.23% in the field and 46.06% in the greenhouse.

Table 4.2. Mean values for yield components and biomass traits of the top two yielding bread wheat parental lines and their direct and reciprocal crosses evaluated at two sites under drought-stressed conditions

Genotypes	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Parents</b>														
<b>BW162</b>	88 15	51 95	35 83	11 50	193 33	56 59	42 16	14 08	517 27	146 15	240 83	64 51	50 69	48 85
<b>LM75</b>	92 55	85 50	47 67	32 25	242 50	352 11	51 96	88 53	560 51	600 12	248 33	136 32	48 83	26 65
<b>Direct Crosses</b>														
<b>BW140 × BW162</b>	85 10	63 50	51 67	20 50	112 50	119 46	14 90	18 11	340 63	257 93	182 25	102 87	55 95	42 89
<b>BW140 × LM75</b>	91 55	51 85	45 17	12 75	260 00	88 03	48 82	13 08	628 62	154 22	273 33	45 40	47 14	32 17
<b>BW141 × BW162</b>	86 20	51 85	35 67	18 00	136 67	169 77	48 04	19 11	352 17	257 74	143 13	58 85	47 06	24 66
<b>BW141 × LM75</b>	93 45	80 90	33 33	30 25	183 33	232 64	33 73	64 39	423 99	487 12	176 87	162 47	45 32	38 43
<b>BW152 × BW162</b>	89 05	57 75	43 00	13 25	100 00	163 48	23 33	142 85	347 58	357 39	191 67	43 64	59 11	20 34
<b>BW152 × LM75</b>	96 60	70 60	41 17	29 75	208 33	213 78	32 55	33 20	536 31	335 55	252 50	75 70	50 12	25 04
<b>BW162 × LM26</b>	90 75	78 90	37 50	31 00	135 83	352 11	15 49	131 79	337 55	686 34	159 17	173 03	49 42	31 20
<b>BW162 × LM47</b>	87 90	75 00	28 83	27 50	140 83	270 37	26 27	52 31	280 21	468 78	96 67	124 87	38 07	29 98
<b>BW162 × LM48</b>	83 75	77 10	35 33	35 75	110 00	326 96	36 47	76 46	332 70	559 81	159 17	133 67	53 73	27 65
<b>BW162 × LM70</b>	92 15	72 00	35 83	27 75	116 67	62 88	35 10	44 26	322 43	150 44	145 87	-	50 77	-
<b>BW162 × LM71</b>	88 50	49 05	37 83	13 00	138 33	69 16	18 24	11 07	317 44	133 64	137 50	45 65	45 96	37 24
<b>BW162 × LM75</b>	98 10	85 95	38 50	38 00	221 67	282 94	30 59	97 58	562 30	512 65	265 00	112 93	49 84	27 21
<b>LM26 × LM75</b>	91 65	82 25	36 33	30 75	126 67	295 52	31 18	75 45	354 48	505 45	168 07	114 94	51 99	26 73
<b>LM47 × LM75</b>	90 85	73 25	31 67	20 50	185 83	238 93	33 53	29 17	407 09	379 48	160 45	95 19	42 95	27 17
<b>LM48 × LM75</b>	85 70	53 90	48 00	17 75	153 33	94 31	8 63	28 17	322 36	195 16	188 33	62 12	60 03	37 20
<b>LM70 × LM75</b>	95 50	94 30	48 17	34 50	147 50	383 54	9 80	49 29	382 72	562 46	192 67	110 79	51 67	21 59
<b>LM71 × LM75</b>	92 00	72 15	39 33	22 25	167 50	201 20	39 61	37 22	436 12	342 74	195 73	89 16	49 36	29 18
<b>Reciprocal Crosses</b>														
<b>BW162 × BW140</b>	88 25	58 10	43 83	16 50	190 83	150 90	24 31	74 45	545 96	353 64	208 33	109 66	39 94	39 28
<b>BW162 × BW141</b>	88 65	81 20	36 17	29 25	115 83	245 22	22 16	64 39	312 52	459 82	149 17	128 39	51 37	32 47
<b>BW162 × BW152</b>	81 25	79 70	32 33	29 75	194 17	295 52	27 84	88 53	409 21	502 19	160 00	100 98	41 95	24 41
<b>LM26 × BW162</b>	82 55	73 75	39 33	29 00	224 17	320 67	46 67	54 32	476 56	519 92	175 83	123 87	40 90	26 60
<b>LM47 × BW162</b>	93 55	72 80	32 50	24 25	145 00	207 49	23 33	50 30	300 93	357 69	113 33	85 39	40 82	27 78
<b>LM48 × BW162</b>	87 00	79 00	40 00	29 50	100 00	264 08	24 90	63 38	335 50	543 31	180 00	132 04	57 95	27 51
<b>LM70 × BW162</b>	84 10	73 05	36 00	31 75	95 83	251 50	50 39	56 34	428 18	448 79	240 98	120 47	63 79	30 70
<b>LM71 × BW162</b>	83 15	74 25	34 50	25 00	105 00	220 07	22 16	125 75	378 33	457 93	127 50	95 82	35 80	28 85
<b>LM75 × BW140</b>	95 75	60 85	36 33	15 50	202 50	169 77	62 16	32 19	538 63	299 50	234 17	83 37	49 15	31 19
<b>LM75 × BW141</b>	86 45	72 65	36 83	31 75	149 17	276 65	11 37	46 28	391 61	523 76	197 50	171 65	51 94	35 95
<b>LM75 × BW152</b>	82 65	82 70	42 50	33 00	111 67	289 23	20 20	62 37	335 64	518 69	174 17	141 09	55 21	30 92
<b>LM75 × BW162</b>	93 75	68 70	41 50	20 00	126 67	226 35	36 86	23 14	408 25	343 66	209 17	80 48	56 32	25 11
<b>LM75 × LM26</b>	87 55	61 50	40 00	18 25	130 00	75 45	20 78	40 24	329 15	175 28	152 45	50 93	49 44	37 71
<b>LM75 × LM47</b>	96 90	85 40	36 50	35 50	200 00	377 26	29 22	168 00	496 37	694 01	228 33	127 14	48 88	24 17
<b>LM75 × LM48</b>	92 40	439 80	41 17	30 75	160 00	295 52	50 78	54 32	525 67	402 37	269 13	44 89	56 67	12 90
<b>LM75 × LM70</b>	101 90	75 00	46 33	23 25	125 00	220 07	10 98	24 14	363 16	379 13	194 17	115 31	55 13	32 48
<b>LM75 × LM71</b>	85 60	82 50	30 67	34 25	163 33	440 13	25 10	97 58	282 03	617 46	80 00	68 16	31 14	13 11
<b>Mean</b>	89 39	73 32	39 85	24 87	150 48	224 89	29 83	59 24	391 10	399 75	178 99	101 21	48 52	34 03
<b>LSD (5%)</b>	13 49	13 49	11 27	11 27	142 30	142 30	33 76	33 76	250 60	250 60	95 90	95 90	8 40	8 40
<b>SEM</b>	0 71	0 71	0 48	0 48	5 52	5 52	1 51	1 51	9 04	9 04	3 37	3 37	0 66	0 66
<b>CV (%)</b>	8 85	8 85	14 71	14 71	29 59	29 59	39 55	39 55	23 50	23 50	23 87	23 87	29 44	29 44

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index, GH = greenhouse, LSD = least significant difference, SEM = standard error of mean, CV = coefficient of variance

Table 4.3. Mean values for yield components and biomass traits of the top two yielding bread wheat parental lines and their direct and reciprocal crosses evaluated at two sites under non-stressed conditions

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Parents</b>														
<b>BW162</b>	99 05	87 20	50 00	27 75	169 17	446 42	31 37	22 13	616 67	927 30	355 67	392 09	60 77	43 32
<b>LM75</b>	101 85	83 30	42 33	28 75	133 33	345 82	56 67	43 26	595 99	768 82	347 00	324 57	64 34	44 73
<b>Direct Crosses</b>														
<b>BW140 × BW162</b>	113 20	70 45	38 67	30 00	168 33	282 94	59 22	28 17	535 65	733 37	263 33	360 91	55 27	51 18
<b>BW140 × LM75</b>	95 45	75 65	43 00	20 25	258 33	465 28	59 61	77 46	719 31	1116 25	343 05	445 54	52 00	42 89
<b>BW141 × BW162</b>	92 05	79 40	47 50	33 75	153 33	220 07	24 90	26 16	473 11	578 29	252 03	283 82	56 23	51 40
<b>BW141 × LM75</b>	103 65	87 20	52 83	34 25	195 00	414 98	20 39	19 11	638 00	546 55	361 20	134 81	58 48	25 56
<b>BW152 × BW162</b>	94 40	67 30	46 83	29 50	176 67	163 48	15 88	20 12	564 08	336 76	317 55	130 91	57 93	41 34
<b>BW152 × LM75</b>	102 70	75 85	45 83	35 50	303 33	301 80	55 88	33 20	774 57	899 25	355 00	482 26	49 40	55 69
<b>BW162 × LM26</b>	98 35	68 55	56 00	28 75	254 17	226 35	28 82	47 28	672 21	416 94	332 67	122 48	51 71	33 13
<b>BW162 × LM47</b>	104 40	64 60	46 83	24 00	195 83	257 79	46 67	21 13	518 82	588 77	264 83	264 83	46 65	46 65
<b>BW162 × LM48</b>	96 60	73 45	58 50	37 00	201 67	339 53	22 55	47 28	560 94	733 89	287 80	296 65	53 46	43 21
<b>BW162 × LM70</b>	96 45	48 25	39 50	10 50	154 17	50 30	22 16	5 03	453 75	87 99	237 12	-	54 94	-
<b>BW162 × LM71</b>	93 05	87 85	41 50	35 00	196 67	471 57	25 69	26 16	650 28	1126 74	365 75	566 64	58 56	51 49
<b>BW162 × LM75</b>	98 90	90 80	52 33	27 00	220 00	427 56	28 04	46 28	637 90	890 80	333 22	539 10	54 64	63 84
<b>LM26 × LM75</b>	98 00	84 80	43 83	31 00	192 50	509 30	40 00	40 24	644 36	1263 71	352 02	610 40	58 25	49 89
<b>LM47 × LM75</b>	104 50	79 60	38 67	31 00	210 00	276 65	15 29	43 26	449 54	727 61	191 67	348 46	44 14	50 92
<b>LM48 × LM75</b>	97 15	81 55	57 50	35 50	129 17	421 27	28 24	23 14	462 89	1068 53	261 10	533 44	60 07	51 03
<b>LM70 × LM75</b>	108 35	86 50	48 17	28 00	239 17	503 01	37 25	57 34	679 43	1215 52	344 45	559 97	53 64	48 35
<b>LM71 × LM75</b>	98 85	73 45	53 83	24 75	261 67	565 88	59 61	27 16	808 99	1229 09	416 85	543 63	55 63	45 23
<b>Reciprocal Crosses</b>														
<b>BW162 × BW140</b>	93 15	58 65	45 83	22 00	160 00	176 05	26 08	6 04	546 61	411 46	308 15	196 05	59 20	48 36
<b>BW162 × BW141</b>	107 00	83 45	48 50	29 25	180 00	352 11	33 73	117 70	595 09	957 99	325 95	417 25	58 06	49 66
<b>BW162 × BW152</b>	97 15	84 05	44 33	31 50	227 50	257 79	30 78	76 46	609 87	679 27	300 50	294 89	51 89	48 92
<b>LM26 × BW162</b>	95 40	80 75	54 50	33 00	170 83	358 39	32 94	36 22	547 74	926 78	293 98	454 85	57 11	51 07
<b>LM47 × BW162</b>	101 75	72 95	47 67	26 75	195 83	213 78	25 88	56 34	521 33	498 90	256 08	195 54	51 69	44 18
<b>LM48 × BW162</b>	98 80	-	58 00	0 00	213 33	427 56	20 00	2 01	590 89	-	305 60	-	53 53	-
<b>LM70 × BW162</b>	91 40	77 75	47 17	25 50	127 50	301 80	20 98	31 19	450 87	502 47	258 45	152 16	60 12	32 29
<b>LM71 × BW162</b>	99 15	78 35	44 00	27 50	340 83	408 69	45 10	18 11	947 08	714 00	479 62	245 47	53 17	35 27
<b>LM75 × BW140</b>	97 60	74 60	47 33	30 50	192 50	333 24	42 75	18 11	615 22	755 81	324 77	345 69	56 73	46 86
<b>LM75 × BW141</b>	95 60	76 85	51 17	32 75	148 33	314 38	29 41	37 22	446 18	892 45	229 43	462 26	55 05	54 05
<b>LM75 × BW152</b>	107 45	79 20	47 33	36 50	226 67	301 80	33 73	30 18	670 40	866 95	350 43	457 23	55 04	54 64
<b>LM75 × BW162</b>	100 00	78 80	50 00	18 75	205 83	396 12	23 92	42 25	622 70	780 45	335 85	292 37	56 09	39 61
<b>LM75 × LM26</b>	102 80	76 15	58 17	26 00	209 17	339 53	22 16	30 18	582 87	945 28	300 47	491 94	53 59	53 76
<b>LM75 × LM47</b>	110 00	81 50	53 50	21 00	198 33	257 79	29 02	27 16	650 91	573 77	362 02	246 85	58 21	45 16
<b>LM75 × LM48</b>	94 10	72 50	46 17	26 00	177 50	389 83	19 22	29 17	578 19	504 67	326 05	239 81	58 33	50 43
<b>LM75 × LM70</b>	90 90	92 10	46 17	30 75	124 17	333 24	22 16	34 20	310 16	746 90	140 03	324 31	48 62	45 50
<b>LM75 × LM71</b>	95 60	73 45	59 83	28 00	219 17	427 56	38 43	54 32	677 24	850 15	358 67	314 76	56 15	39 55
<b>Mean</b>	98 77	79 26	49 31	27 27	191 57	325 71	30 01	33 18	572 50	727 14	299 66	511 52	55 23	46 06
<b>LSD (5%)</b>	13 64	13 64	12 25	12 25	141 90	141 90	31 26	31 26	342 70	342 70	183 10	183 10	8 40	8 40
<b>SEM</b>	0 64	0 64	0 58	0 58	6 97	6 97	1 24	1 24	15 71	15 71	7 87	7 87	0 49	0 49
<b>CV (%)</b>	7 27	7 27	14 96	14 96	27 21	27 21	40 07	40 07	24 41	24 41	25 37	25 37	18 67	18 67

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index, GH = greenhouse, LSD = least significant difference, SEM = standard error of mean, CV = coefficient of variance

### 4.3.3 Combining ability analysis for individual test environments

The combining ability and maternal effects, GCA/SCA ratio and heritability estimates for the individual environments are shown in Table 4.4. Significant GCA effects were observed for PH, KPS and SB at both sites and for PB and GY in the field and greenhouse under drought-stressed conditions. The SCA, reciprocal and non-maternal effects were important for PH, SB, RB and PB in the greenhouse condition. In the field, KPS had significant SCA and non-maternal effects, while only RB had significant reciprocal effects. Significant maternal effects were observed for RB only in the greenhouse. The GCA/SCA ratio was  $>0.5$  for PH, SB, PB and GY under field conditions. Broad sense heritability estimates were relatively low for all traits, with KPS (0.26) and PH (0.33) having relatively the highest values in the field and greenhouse conditions, respectively. Under non-stressed conditions, all recorded traits had significant GCA effects except GY and RB in the field and greenhouse, respectively. There were significant SCA effects for PH and KPS in the field and for PH, SB, PB and GY in the greenhouse. Reciprocal and non-maternal effects were significant in the greenhouse for SB, RB, PB and GY and for PH in the field. Notably, maternal effects were significant in influencing SB in both environments and PB in the greenhouse. The GCA/SCA ratio was close to 0.50 for SB and PB in the field and for RB at both sites. The rest of the traits had GCA/SCA ratios of  $<0.50$ . All traits showed low  $H^2$  with the highest being for PH and KPS in the field.

Table 4.4. Summary mean squares and significant tests of combining ability and maternal effects, Bakers ratio (1978) and heritabilities of individual environments for yield components and biomass traits for a full diallel cross evaluated under drought-stressed and non-stressed conditions at two sites

Drought-stress															
SOV	Df	PH		KPS		SB		RB		PB		GY		HI	
		Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>GCA</b>	9	212 04*	767 19***	208 31***	161 14*	8710 88*	28367 83*	144 66	472 2	45615 91*	41036 56	12280 92	4780 07*	94 11*	420 27***
<b>SCA</b>	45	70 96	226 61**	112 45**	79 35	3271 83	18543 89*	301 44	1642 05**	21139 53	56405 39**	6608 2	2946 51	69 67*	170 87*
<b>REC</b>	45	61 7	201 74**	78 46	66 92	4284 15	21218 72**	378 02*	1608 49**	22019 46	44498 34*	5947 43	1784 35	114 69***	154 81*
<b>Mat</b>	9	43 25	172 48	35 55	64 11	5335 03	7085 38	264 9	2093 48**	14705 64	31262 41	2621 69	1645 63	148 06**	66 17
<b>Nmat</b>	36	66 31	209 05**	89 18*	67 62	4021 43	24752 05**	406 30*	1487 24**	23847 91	47807 32*	6778 87	1819 03	106 35***	176 97*
<b>Residual</b>	80	62 18	105 06	53 24	61 84	3430 41	11256 21	224 13	746 15	22131 93	25858 57	6698 23	2328 08	41 89	93 8
<b>GCA/SCA</b>		0 78	0 37	0 23	0 38	1 67	0 2	0 22	0 05	2 48	0 04	1 77	0 28	0 46	0 44
<b>H<sup>2</sup></b>		0 14	0 33	0 26	0 13	0 07	0 15	0 07	0 21	0 05	0 20	0 08	0 11	0 13	0 19

Non-stress															
SOV	Df	PH		KPS		SB		RB		PB		GY		HI	
		Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>GCA</b>	9	273 92***	601 02***	116 84**	326 46**	8395 10*	42161 17**	719 45**	283 25	52024 43**	241266 67**	10549 19	63460 16**	39 2	50 51
<b>SCA</b>	45	65 27**	216 21*	93 97***	146 99	3629 75	29439 46**	281 43	655 69	21648 6	134111 78*	7451 72	37670 76*	31 59	139 33
<b>REC</b>	45	57 37*	145 98	50 74	133 41	4620 2	36717 56***	225 37	1179 77*	18407 47	198289 23***	5436 46	50828 98***	46 60**	146 3
<b>Mat</b>	9	45 81	248 05	64 87	135 82	6611 56*	61623 24***	254 9	524	17933 02	188613 90*	3242 18	33784 41	55 64*	118 67
<b>Nmat</b>	36	60 26*	120 47	47 21	132 81	4122 36	30491 15*	217 99	1343 71**	18526 08	200708 06**	5985 03	55090 13***	44 34**	153 21
<b>Residual</b>	80	32 1	130 55	34 28	106 77	3277 85	14585 88	224 9	600 05	18517 75	82968 53	6369 35	21675 35	21 72	95 59
<b>GCA/SCA</b>		0 43	0 42	0 13	0 41	0 52	0 17	0 52	0 57	0 49	0 31	0 35	0 3	0 19	0 09
<b>H<sup>2</sup></b>		0 33	0 24	0 29	0 14	0 08	0 19	0 15	0 03	0 12	0 16	0 06	0 16	0 07	0 11

SOV = source of variation, df = degrees of freedom, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass (g m<sup>-2</sup>) RB = root biomass, (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>) and GY = grain yield (g m<sup>-2</sup>), GCA = general combining ability, SCA = specific combining ability effects, REC = reciprocal effects, MAT = maternal effects, NMAT = non-maternal effects, GH = greenhouse

#### **4.3.4 Combining ability analysis across sites**

Parental lines had significant ( $P < 0.05$ ) GCA effects for all recorded traits (Table 4.5). Significant SCA effects among  $F_2$  families were observed for PH, KPS, SB, RB and PB. Reciprocal effects were significant for KPS and biomass traits such as SB, RB and PB with reciprocal crosses showing significant maternal effects only for KPS. The GCA  $\times$  site interaction effects were significant for parents for PH, KPS, SB and PB. Similarly, SCA  $\times$  site effects for families were significant for the same traits in addition to RB and GY. Reciprocal effects had significant interaction with sites for all traits except KPS. Maternal effects and site interaction influenced SB, RB and GY.

Table 4.5. Summary mean squares and significant tests of combining ability and maternal effects for yield components and biomass traits for a full diallel cross evaluated at two sites under drought-stressed and non-stressed conditions

SOV	df	PH	KPS	SB	RB	PB	GY	HI
<b>GCA</b>	9	1104.56***	489.32***	38611.16***	991.03*	184560.88***	44512.71***	186.07**
<b>SCA</b>	45	211.14***	158.52***	16617.53***	854.09***	61371.66*	12159.74	109.09**
<b>REC</b>	45	117.16	107.37**	16470.40***	732.57*	66898.10**	12986.27	115.99**
<b>Mat</b>	9	103.9	156.02**	11323.91	842.36	67828.25	16364.47	137.25*
<b>Nmat</b>	36	120.48	95.21*	17757.03*	705.12*	66665.57**	12141.72	110.68*
<b>GCA × Site</b>	9	355.85***	281.28***	19824.58*	245.37	75250.72*	13887.63	166.48**
<b>SCA × Site</b>	45	135.69*	139.83***	14154.26**	723.30*	67335.00**	15823.51**	94.50*
<b>REC × Site</b>	45	132.27*	87.93	23688.23***	1070.41***	101235.89***	21979.20***	113.14**
<b>MAT × Site</b>	9	116.18	50.42	24089.61**	1211.20**	58512.87	10269.3	85.97
<b>NMAT × Site</b>	36	136.29*	97.30*	23587.89***	1035.22***	111916.64***	24906.68***	119.93**
<b>Residual</b>	522	85.16	63.09	8805.42	460.3	38876.5	9826.45	67.51

SOV = source of variation, df = degrees of freedom, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ) RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), GCA = general combining ability, SCA = specific combining ability effects, REC = reciprocal effects, MAT = maternal effects, NMAT = non-maternal effects

#### **4.3.5 General combining ability effects**

The general combining ability of parental genotypes are shown in Table 4.6 for drought-stressed and non-stressed conditions. Under drought stress, parent BW141 had negative GCA effects for PH at both sites and positive GCA effects on GY in the greenhouse condition. Parental line LM26 showed significant and positive GCA effects for KPS with negative GCA's for lines BW140 and LM47. No parents showed significant GCA effects for RB. The GCA effects for SB, PB and GY were significant in a desirable direction for LM75 in the field. Parental lines LM70 had positive GCA effects on PH, SB and PB in the greenhouse. Under non-stressed conditions, BW140 maintained negative GCA effects for PH and PB while LM47 showed significant positive effects for PH in the field. The GCA effects for KPS were strong and positive for LM48 at both sites. Negative GCA effects for RB were observed in the field for lines LM48 and LM70. Genotype LM75 showed positive GCA effects for RB in the field and PH, SB, PB and GY in the greenhouse.

#### **4.3.6 Specific combining ability and reciprocal effects**

The SCA effects of direct crosses are shown in Appendix 4.3. Similar to the GCA effects of parental lines, no families maintained positive SCA effects for all the recorded traits across the sites. Positive SCA effects were observed for BW141 × BW152 for PH under drought and for BW141 × LM47 under non-stress condition. The families BW140 × LM47 and LM48 × LM71 had positive SCA effects for RB at both sites under drought-stressed and non-stressed conditions, respectively. Significant SCA effects were observed for BW162 × LM26 for SB, RB, PB and GY under drought, and BW140 × LM75 for the same traits under non-stressed conditions. Family BW140 × BW152 had positive SCA effects in the greenhouse and negative SCA effects in the field for KPS, SB, RB, PB and GY under drought conditions. Significant SCA effects were observed for BW162 × LM48 under non-stressed conditions. Strong reciprocal effects were recorded in the families LM47 × BW152, LM26 × BW140 and LM75 × LM47 under drought-stressed conditions (Appendix 4.4).

Table 4.6. Estimates of general combining ability effects for yield components and biomass traits of 10 bread wheat parental lines evaluated under drought-stressed and non-stressed conditions in the field and greenhouse

Drought-stress														
Parent	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>BW140</b>	-2.32	-6.03**	2.15	-4.03**	5.68	-43.79*	1.99	-1.03	33.08	-38.12	16.42	5.2	0.50	3.97*
<b>BW141</b>	-2.97*	-4.30*	-0.06	-0.87	-8.90	-17.69	-0.61	-8.67	-30.35	9.94	-13.03	20.27*	-0.48	4.18*
<b>BW152</b>	-0.50	-0.14	-2.64*	-0.02	-0.78	8.4	-1.78	-0.02	-8.42	-16.14	-6.60	-5.72	-0.90	-1.05
<b>BW162</b>	-1.39	-1.12	-2.25	-0.72	-5.65	-18.32	0.91	0.88	-3.71	-18.90	-4.40	-2.3	0.15	0.19
<b>LM26</b>	0.46	-2.4	4.37**	1.35	6.23	-15.49	0.75	1.04	7.40	-0.75	7.37	12.21	0.16	4.45*
<b>LM47</b>	3.92**	0.19	-2.67*	-0.58	16.73	11.54	0.58	1.99	3.87	-4.02	-11.72	-11.7	-2.73*	-1.42
<b>LM48</b>	-1.48	-0.53	1.71	1.4	-26.15*	-9.71	-3.82	-0.27	-46.05	-8.16	-11.41	-5.52	3.21*	0.56
<b>LM70</b>	2.29	9.02***	-0.71	2.65	1.77	47.51*	-1.45	-0.02	2.59	61.25*	1.71	4.05	1.03	-4.09*
<b>LM71</b>	-0.79	-0.07	-0.48	-1.5	-13.82	6.2	1.10	1.39	-29.71	-32.03	-18.33	-16.33	-1.02	-2.49
<b>LM75</b>	2.79*	5.38**	0.59	2.31	24.89*	31.35	2.33	4.71	71.30*	46.93	40.00**	-0.15	0.07	-4.30*

Non-stress														
Parent	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>BW140</b>	-3.77**	-6.19**	0.53	-2.83	-14.73	-22.06	-1.31	1.23	-49.65*	-45.40	-16.91	-17.53	-0.55	0.46
<b>BW141</b>	1.68	-2.00	-0.47	-1.77	-3.98	-51.48*	-0.95	-1.49	-27.44	-93.35	-12.16	-44.29	-0.72	0.65
<b>BW152</b>	-0.16	1.28	-1.92	1.70	-4.44	21.64	-1.21	3.29	-22.91	64.07	-18.25	17.97	-0.70	0.27
<b>BW162</b>	-0.30	0.88	-0.93	0.99	2.48	-18.10	0.95	1.73	24.97	-56.60	16.39	-22.15	1.25	0.08
<b>LM26</b>	-1.28	1.51	1.42	0.86	20.77*	29.82	3.92	-0.28	43.27	60.76	22.64	32.96	-0.39	-1.45
<b>LM47</b>	5.75***	1.68	-0.50	-2.75	6.39	-28.85	-0.54	-1.99	5.74	-82.54	-2.42	-40.11	-0.84	-1.97
<b>LM48</b>	-2.66*	2.91	4.08**	5.58**	-26.53*	13.59	-5.76*	-1.39	-35.26	35.86	-9.73	22.74	2.14*	0.39
<b>LM70</b>	-0.62	3.03	-1.40	0.36	-6.28	-5.77	-6.36*	-4.36	-23.83	-45.66	-12.60	-28.22	-0.30	-1.37
<b>LM71</b>	-0.13	-7.40**	-0.51	-2.88	19.02	0.89	4.19	-1.39	43.20	14.71	13.29	-4.89	-0.39	0.45
<b>LM75</b>	1.50	4.31*	-0.30	0.75	7.31	60.31**	7.07*	4.65	41.91	148.15**	19.74	83.52**	0.50	2.50

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ) RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), GH = greenhouse

#### 4.4 Discussion

Significant differences were observed among the tested families thereby revealing substantial variation for PH, RB, SB, PB and GY. This offers an opportunity for an effective selection of biomass traits to improve drought tolerance and enhance carbon sequestration of cultivars for sustainable wheat production. Interaction of families by site showed that genotype ranking changed in the different sites indicating strong genotype by environment interaction affecting all the measured traits. Among all the traits, GY was subject to interaction effect of families and water regime. This suggests that GY is more sensitive to moisture fluctuations and genotype by environment interactions than the other traits, and this may affect selection response to achieve drought-tolerance (Cohen et al., 2021; Qaseem et al., 2019). Therefore, to achieve yield stability, genotypes should be evaluated across multiple growin×environments with different moisture availability to identify stable and drought-tolerant genotypes for water-limited environments (Chiipanthenga et al., 2021).

Harvest index (HI) is an important trait used for selection of high yielding cultivars for both irrigated and dry environments. According to Rivera-Amado et al., (2019), HI in modern wheat cultivars ranges from 50 – 55% for winter wheat and 45 – 50% for spring wheat. In a panel of genotypes introduced in the UK between 1972 and 1995, genetic gains were strongly influenced by HI in earlier years (1972 – 1983) but by above-ground biomass in the latter years (1983 – 1995) (Shearman et al., 2005). Similar results have been observed in other studies (Foulkes et al., 2011; Sanchez-Garcia et al., 2013; Silva et al., 2014; Rivera-Amado et al., 2019). With yield in modern wheat cultivars still sink limited, there is opportunity to further increase HI by improving the sink capacity of spikes to the theoretical maximum of 65% (Foulkes et al., 2011). It is therefore important that plant breeders should target high biomass production to increase radiation use efficiency while maximizing harvest index to ensure greater partitioning of photo-assimilates to the grain (Rivera-Amado et al., 2019). In addition, enhanced total biomass production will ensure that high yielding genotypes showing high harvest index will have stronger stems and roots to support the plant structure from lodging in heavier yielding genotypes (Reynolds et al., 2011). In the present panel of tested genotypes, segregation among the families may have reduced the wide variability in HI as shown in the absence of significant effects for HI. However, identification of transgressive segregants in advanced families will allow selection of high yielding wheat cultivars

with maximised harvest index and high biomass production both under drought-stressed and non-stressed conditions.

All other traits, including PH, KPS, SB, PB and GY were severely and negatively affected by drought stress. However, individual genotypes responded to drought stress differently, with some parents and families showing high levels of drought tolerance compared to the others. The different phenotypic performances observed allow for targeted selection of better-performing families for genetic advancement, while parental lines can be selected to develop new breeding populations for either dryland or irrigated wheat production (Shamuyarira et al., 2019). Some families, including BW141 × LM26, LM47 × BW152 and LM26 × BW140 scored higher than all the parental genotypes for RB, PB and GY, respectively, indicating that the parental genotypes were able to transmit favourable genes to their progeny under contrasting levels of soil moisture availability.

Evaluation of the test genotypes was done at contrasting growing conditions, namely: greenhouse; and field environments. Data on the assessment of families in the greenhouse using pot experiments were included to capture and assess total root biomass in the pots, while it cannot be completely recovered in field experiments. In addition, root evaluation in pot experiments and growth chambers is easier and more accurate as there is no mixture of roots from adjacent plants or different genotypes when collecting root samples (Amos and Walters 2006). In this study, plants allocated more biomass below ground to promote denser and deeper root growth for efficient water and nutrient uptake under drought-stressed conditions (Ober et al., 2021). However, this increase in RB production was high in the greenhouse and small in the field, indicating greater accuracy of greenhouse trials in studies involving root phenotyping. Different drought-induced root growth responses have been observed between greenhouse and field conditions under different stress severity (Li et al., 2021). Many confounding environmental effects in field trials compared to greenhouse trials may contribute to the low accuracy of root phenotyping in the field (Ho et al., 2005).

The significance of maternal effects for SB under non-stressed conditions showed that a portion of the non-additive gene action in the population could be captured by choice of the parents used as a male or female in the mating design. The Baker's (1978) ratio was slightly higher under drought-stressed conditions than under non-stressed conditions showing that water availability was able to alter the proportion of additive and non-additive gene action affecting the traits of interest.

Similar results were observed by Chiipanthenga et al. (2021) in soybean. The Baker's ratio (1978) was  $> 0.5$  for PH, SB, PB and GY under drought-stressed conditions. These traits can be improved by exploiting additive gene action at early generations, thereby increasing selection efficiency (Mohammadi et al., 2021). Several studies have reported quantitative trait loci (QTL) with additive gene effects for GY and related traits, allowing for the selection of transgressive progenies by crossing superior parents (Zhang et al., 2010; Mwadingeni et al., 2018; Mohammadi et al., 2021). Conversely, under non-stressed conditions, there was a greater influence of non-additive gene action, which opens an opportunity to exploit dominance and epistasis for hybrid breeding in irrigated environments (Sharshar and Genedy 2020). The heritability estimates were low for all measured traits indicating that the phenotype was a poor measure of the genetic merit of the evaluated lines and families, which reduces the effectiveness of selection. Similarly, low heritability values have been reported in other studies (Collaku and Harrison 2005; Manal 2009).

The presence of interaction effects of sites with combining ability and maternal effects for the majority of measured traits highlights the confounding effects of the environment on gene expression and the importance of choosing the correct selection environment to assess the genotypic value of genotypes. The environments showed that RB had significant reciprocal effects under drought-stressed conditions across sites. Based on those observations, choosing a male or female parent is important to ensure the inheritance of maternal genes for improved root biomass under drought-stress. Strong reciprocal effects influencing root traits have been reported in wheat for different abiotic stresses such as salt stress (Aycañ et al., 2021) and cold stress (Skinner et al., 2019). Also, in a study evaluating interspecific hybrids of sunflower, Hernández et al., (2021) reported reciprocal effects on root traits that extended beyond the seedling stage and were expressed in mature individuals. Under non-stressed conditions, the maternal effects were observed for PH, SB, RB, PB and GY but were inconsistent across different sites, thereby limiting the usefulness of these effects for breeding purposes.

The GCA effects of parents change from positive to negative for all recorded traits across the test conditions. This suggests that the environment can influence gene expression and heritability in individual genotypes. Parental line LM75 maintained GCA effects in a positive direction for SB, RB, PB and GY. It was the only genotype with a positive effect observed for root biomass under field conditions. This genotype can be utilized to transmit additive quantitative trait loci for the

improvement of biomass production and overall yield potential. Different genotypes had significant positive GCA effects for KPS under drought-stressed (LM26) and non-stressed (LM48) conditions. Thus, the genetic merit of an individual for KPS can only be maintained under specific soil moisture conditions, thus, limiting the usefulness of the above-mentioned parental lines in breeding for increased kernel number under different environmental conditions. Employing several cycles of recurrent selection to increase the allele frequencies of favorable genes for KPS in the current genetic material may be warranted (Mwadzingeni et al., 2018).

The deviations in the expected performance of families as revealed by their SCA's varied greatly among the different sites and water regimes. This confounds the identification and selection of families and individual plants for genetic advancement. However, transgressive phenotypes with high SCA effects are highly heritable, if they involve parents with high GCA effects (Mwadzingeni et al., 2018). This is important to increase the adaptability of advanced material in water-limited and low-input environments, where parental genotypes perform poorly (Mackay et al., 2021). Families such as BW141 × LM26 with high SCA effects and at least one parental genotype with high GCA effects for biomass traits and GY may be selected for genetic advancement for drought-prone areas. In addition, reciprocal crosses LM47 × BW152, LM26 × BW140 and LM75 × LM47 with significant reciprocal effects for root biomass and grain yield should also be selected. These genotypes will contribute to soil carbon build-up while concurrently increasing the resilience of wheat productivity in low-input agricultural systems.

#### **4.5 Conclusions**

Significant genetic variation for grain yield, yield-related traits and biomass allocation was observed for the assessed parental genotypes and their families. Additive gene effects conditioned PH, SB, PB and GY under drought, whereas under non-stressed conditions non-additive gene action was more predominant. Strong maternal and reciprocal genetic effects were recorded for RB across the testing sites under drought-stressed conditions. Genotype LM75 maintained GCA effects in a positive and desirable direction, and it can be selected for population development in breeding programmes. Early generation selection using PH, SB, PB and GY is recommended to improve drought tolerance by exploiting additive gene action under drought conditions. Higher RB production may be maintained by a positive selection of male and female parents to capture the significant maternal and reciprocal effects found in this study.

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Appendix 4.1. Mean values for yield components and biomass traits of 10 bread wheat parental lines, 45 direct and 45 reciprocal crosses evaluated at two sites under drought-stressed conditions

Genotypes	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Direct crosses</b>														
<b>BW140 × BW141</b>	71.75	50.30	41.50	18.00	99.17	144.61	18.04	22.13	302.46	297.55	158.33	111.79	55.67	40.59
<b>BW140 × BW152</b>	94.45	66.75	32.83	23.75	142.50	326.96	16.47	109.66	346.17	458.66	160.00	158.57	48.53	45.44
<b>BW140 × BW162</b>	85.10	63.50	51.67	20.50	112.50	119.46	14.90	18.11	340.63	257.93	182.25	102.87	55.95	42.89
<b>BW140 × LM26</b>	87.25	69.65	36.00	21.75	175.00	125.75	26.08	22.13	384.38	266.91	156.67	101.73	43.73	41.56
<b>BW140 × LM47</b>	80.70	78.20	29.00	24.75	135.00	326.96	41.18	97.58	324.38	564.02	126.67	119.21	44.73	25.56
<b>BW140 × LM48</b>	85.50	61.00	49.83	18.25	168.33	81.74	22.94	23.14	436.00	181.68	209.17	65.64	50.64	41.40
<b>BW140 × LM70</b>	98.10	63.10	43.33	24.50	143.33	144.61	56.08	39.23	451.39	287.87	215.37	88.91	54.48	35.76
<b>BW140 × LM71</b>	88.20	64.75	57.00	22.50	215.83	100.60	39.61	26.16	585.97	203.16	282.50	-	51.71	-
<b>BW140 × LM75</b>	91.55	51.85	45.17	12.75	260.00	88.03	48.82	13.08	628.62	154.22	273.33	45.40	47.14	32.17
<b>BW141 × BW152</b>	98.55	65.50	43.17	23.70	186.67	163.48	34.90	33.20	467.91	316.73	210.55	102.61	48.62	36.19
<b>BW141 × BW162</b>	86.20	51.85	35.67	18.00	136.67	169.77	48.04	19.11	352.17	257.74	143.13	58.85	47.06	24.66
<b>BW141 × LM26</b>	102.10	49.75	54.17	21.25	267.50	81.74	85.69	9.05	670.76	191.87	271.43	86.39	46.39	47.25
<b>BW141 × LM47</b>	94.35	48.40	37.50	19.75	171.67	37.73	26.08	24.14	404.25	119.84	176.50	49.55	46.67	51.78
<b>BW141 × LM48</b>	79.80	58.20	39.67	18.00	79.17	201.20	15.49	21.13	210.68	420.94	99.17	153.42	50.81	38.37
<b>BW141 × LM70</b>	89.80	92.55	41.00	28.25	133.33	584.75	24.12	26.16	344.65	793.79	160.00	156.31	49.92	20.36
<b>BW141 × LM71</b>	84.05	46.05	41.67	12.00	116.67	75.45	45.10	5.03	399.78	121.38	203.43	34.96	57.36	30.05
<b>BW141 × LM75</b>	93.45	80.90	33.33	30.25	183.33	332.64	33.73	64.39	423.99	487.12	176.87	162.47	45.32	38.43
<b>BW152 × BW162</b>	89.05	57.75	43.00	13.25	100.00	163.48	23.33	142.85	347.58	357.39	191.67	43.64	59.11	20.34
<b>BW152 × LM26</b>	94.25	56.70	46.83	13.50	189.17	62.88	32.55	28.17	547.37	146.22	278.33	47.16	54.06	39.95
<b>BW152 × LM47</b>	93.60	60.45	37.83	21.75	127.50	169.77	26.47	46.28	323.17	290.34	144.62	63.50	48.74	26.02
<b>BW152 × LM48</b>	87.30	76.50	41.00	36.25	92.50	264.08	6.67	70.42	267.84	481.48	144.17	125.63	55.20	30.56
<b>BW152 × LM70</b>	84.90	85.10	26.67	23.75	154.17	389.83	16.08	115.69	292.12	616.61	104.17	94.94	37.74	18.95
<b>BW152 × LM71</b>	87.90	79.10	41.17	28.25	101.67	276.65	17.65	70.42	210.40	503.77	77.85	133.93	40.39	30.91
<b>BW152 × LM75</b>	96.60	70.60	41.17	29.75	208.33	213.78	32.55	33.20	536.31	335.55	252.50	75.70	50.12	25.04
<b>BW162 × LM26</b>	90.75	78.90	37.50	31.00	135.83	352.11	15.49	131.79	337.55	686.34	159.17	173.03	49.42	31.20
<b>BW162 × LM47</b>	87.90	75.00	28.83	27.50	140.83	270.37	26.27	52.31	280.21	468.78	96.67	124.87	38.07	29.98
<b>BW162 × LM48</b>	83.75	77.10	35.33	35.75	110.00	326.96	36.47	76.46	332.70	559.81	159.17	133.67	53.73	27.65
<b>BW162 × LM70</b>	92.15	72.00	35.83	27.75	116.67	62.88	35.10	44.26	322.43	150.44	145.87	-	50.77	-
<b>BW162 × LM71</b>	88.50	49.05	37.83	13.00	138.33	69.16	18.24	11.07	317.44	133.64	137.50	45.65	45.96	37.24
<b>BW162 × LM75</b>	98.10	85.95	38.50	38.00	221.67	282.94	30.59	97.58	562.30	512.65	265.00	112.93	49.84	27.21
<b>LM26 × LM47</b>	97.60	72.85	34.67	28.25	169.17	163.48	36.08	37.22	389.52	323.55	157.50	105.00	44.56	36.67
<b>LM26 × LM48</b>	93.45	65.80	61.17	30.00	121.67	144.61	32.55	32.19	383.36	307.02	195.85	111.29	55.83	40.49
<b>LM26 × LM70</b>	92.70	72.65	44.33	25.00	124.17	270.37	17.06	81.49	343.87	448.08	173.20	82.24	53.00	22.43
<b>LM26 × LM71</b>	95.40	79.00	41.17	28.50	174.17	289.23	37.84	52.31	467.71	484.99	218.55	122.61	50.84	28.34
<b>LM26 × LM75</b>	91.65	82.25	36.33	30.75	126.67	295.52	31.18	75.45	354.48	505.45	168.07	114.94	51.99	26.73
<b>LM47 × LM48</b>	99.00	78.35	45.50	25.00	162.50	339.53	15.49	95.57	413.34	553.10	201.15	100.85	50.56	22.04
<b>LM47 × LM70</b>	92.85	78.70	37.17	25.00	222.50	270.37	20.59	56.34	496.59	427.19	216.67	85.89	45.52	23.16
<b>LM47 × LM71</b>	89.10	63.90	40.50	19.00	130.83	326.96	26.08	36.22	306.20	260.90	127.60	52.31	45.55	23.28
<b>LM47 × LM75</b>	90.85	73.25	31.67	20.50	185.83	238.93	33.53	29.17	407.09	379.48	160.45	95.19	42.95	27.17
<b>LM48 × LM70</b>	86.90	83.75	39.17	35.25	85.83	276.65	21.57	96.58	270.23	501.38	139.17	109.53	55.97	27.06
<b>LM48 × LM71</b>	82.95	76.35	35.83	31.50	129.17	314.38	40.20	125.75	301.96	547.83	113.33	92.05	43.30	21.81
<b>LM48 × LM75</b>	85.70	53.90	48.00	17.75	153.33	94.31	8.63	28.17	322.36	195.16	188.33	62.12	60.03	37.20
<b>LM70 × LM71</b>	90.05	89.35	40.17	30.00	163.33	414.98	48.24	81.49	412.28	602.99	171.55	91.04	47.12	17.46
<b>LM70 × LM75</b>	95.50	94.30	48.17	34.50	147.50	383.54	9.80	49.29	382.72	562.46	192.67	110.79	51.67	21.59
<b>LM71 × LM75</b>	92.00	72.15	39.33	22.25	167.50	201.20	39.61	37.22	436.12	342.74	195.73	89.16	49.36	29.18

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

Appendix 4.1 continued

Genotypes	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Reciprocal crosses</b>														
<b>BW141 × BW140</b>	73 95	59 30	26 67	18 25	150 83	100 60	30 59	24 14	281 85	258 34	85 83	114 18	34 16	48 75
<b>BW152 × BW140</b>	79 40	69 25	24 67	18 25	100 83	220 07	21 18	85 51	249 18	465 95	81 67	137 07	35 82	36 03
<b>BW152 × BW141</b>	92 45	77 35	35 17	30 50	121 67	408 69	47 65	82 49	449 14	636 11	239 17	123 87	59 57	22 37
<b>BW162 × BW140</b>	88 25	58 10	43 83	16 50	190 83	150 90	24 31	74 45	545 96	353 64	208 33	109 66	39 94	39 28
<b>BW162 × BW141</b>	88 65	81 20	36 17	29 25	115 83	245 22	22 16	64 39	312 52	459 82	149 17	128 39	51 37	32 47
<b>BW162 × BW152</b>	81 25	79 70	32 33	29 75	194 17	295 52	27 84	88 53	409 21	502 19	160 00	100 98	41 95	24 41
<b>LM26 × BW140</b>	95 65	54 75	49 50	22 50	223 33	176 05	39 41	70 42	675 17	398 75	352 50	130 15	55 45	39 64
<b>LM26 × BW141</b>	79 15	64 15	52 33	25 25	61 67	232 64	10 20	33 20	270 10	455 34	-	161 97	-	38 37
<b>LM26 × BW152</b>	83 55	75 10	31 83	28 75	130 00	213 78	23 14	36 22	296 46	375 64	122 50	107 39	44 82	31 64
<b>LM26 × BW162</b>	82 55	73 75	39 33	29 00	224 17	320 67	46 67	54 32	476 56	519 92	175 83	123 87	40 90	26 60
<b>LM47 × BW140</b>	90 80	67 80	45 83	23 50	180 83	251 50	54 31	98 59	475 97	509 44	205 83	136 19	48 81	33 15
<b>LM47 × BW141</b>	89 70	70 05	25 50	30 00	139 17	220 07	26 86	119 72	326 90	448 66	137 50	93 06	45 83	28 29
<b>LM47 × BW152</b>	98 85	85 40	50 50	31 25	294 17	308 09	60 59	47 28	698 93	490 88	294 17	115 82	46 08	26 11
<b>LM47 × BW162</b>	93 55	72 80	32 50	24 25	146 00	207 49	23 33	50 30	300 93	357 69	113 33	85 39	40 82	27 78
<b>LM47 × LM26</b>	104 25	68 35	40 00	29 25	190 83	194 92	18 24	86 52	387 83	420 47	152 78	118 84	41 34	35 59
<b>LM48 × BW140</b>	93 50	50 75	49 00	18 75	217 50	94 31	38 04	27 16	570 48	223 00	269 18	86 77	50 56	44 31
<b>LM48 × BW141</b>	79 45	60 70	48 67	20 25	180 83	132 04	26 47	22 13	434 48	245 98	194 17	78 47	47 59	35 05
<b>LM48 × BW152</b>	94 15	80 70	29 17	29 25	93 33	308 09	16 27	128 77	257 81	578 99	126 67	121 48	52 44	26 98
<b>LM48 × BW162</b>	87 00	79 00	40 00	29 50	100 00	264 08	24 90	63 38	335 50	543 31	180 00	132 04	57 95	27 51
<b>LM48 × LM26</b>	86 00	67 50	46 17	29 75	110 00	352 11	25 29	73 44	354 67	554 87	187 50	110 54	56 93	22 96
<b>LM48 × LM47</b>	89 85	61 45	34 00	22 75	140 83	100 60	29 41	32 19	383 77	223 57	182 50	77 59	51 50	40 54
<b>LM70 × BW140</b>	93 25	70 35	36 17	16 75	116 67	182 34	13 92	20 12	352 28	312 96	189 48	94 44	56 00	32 25
<b>LM70 × BW141</b>	88 60	78 85	48 17	32 25	200 00	176 05	24 31	37 22	466 11	431 32	206 67	186 36	46 78	47 29
<b>LM70 × BW152</b>	91 00	79 00	42 00	22 50	177 50	226 35	28 82	52 31	569 02	390 04	310 00	95 19	57 39	28 19
<b>LM70 × BW162</b>	84 10	73 05	36 00	31 75	95 83	251 50	50 39	56 34	428 18	448 79	240 98	120 47	63 79	30 70
<b>LM70 × LM26</b>	93 40	64 20	45 00	30 50	219 17	289 23	44 31	64 39	505 75	535 16	207 07	101 86	44 87	21 64
<b>LM70 × LM47</b>	98 95	86 55	36 00	32 50	234 17	339 53	36 08	188 13	518 23	641 09	211 95	96 95	43 96	21 40
<b>LM70 × LM48</b>	91 30	-	23 67	-	128 33	-	22 35	7 04	287 19	-	116 67	-	44 05	-
<b>LM71 × BW140</b>	85 30	65 85	41 67	27 25	113 33	295 52	21 76	36 22	393 84	443 70	221 15	95 70	59 44	23 49
<b>LM71 × BW141</b>	86 05	68 30	36 00	19 50	120 00	201 20	18 24	73 44	275 71	423 69	117 50	127 39	45 64	36 37
<b>LM71 × BW152</b>	94 00	59 50	41 83	16 00	183 33	144 61	47 65	78 47	497 16	262 07	227 50	33 32	50 61	18 15
<b>LM71 × BW162</b>	83 15	74 25	34 50	25 00	105 00	220 07	22 16	125 75	378 33	457 93	127 50	95 82	35 80	28 85
<b>LM71 × LM26</b>	83 50	73 25	35 17	27 25	110 00	289 23	29 41	71 43	297 91	588 12	135 47	194 41	50 45	37 63
<b>LM71 × LM47</b>	91 95	74 90	49 50	18 00	133 33	201 20	35 10	70 42	386 83	322 53	186 67	43 51	53 07	17 26
<b>LM71 × LM48</b>	100 00	75 95	42 83	33 75	78 33	314 38	28 04	53 32	245 80	460 24	119 17	79 10	54 73	19 44
<b>LM71 × LM70</b>	91 00	65 80	31 67	20 00	117 50	176 05	29 41	54 32	346 55	328 22	170 63	83 63	53 80	30 53
<b>LM75 × BW140</b>	95 75	60 85	36 33	15 50	202 50	169 77	62 16	32 19	538 63	299 50	234 17	83 37	49 15	31 19
<b>LM75 × BW141</b>	86 45	72 65	36 83	31 75	149 17	276 65	11 37	46 28	391 61	523 76	197 50	171 65	51 94	35 95
<b>LM75 × BW152</b>	82 65	82 70	42 50	33 00	111 67	289 23	20 20	62 37	335 64	518 69	174 17	141 09	55 21	30 92
<b>LM75 × BW162</b>	93 75	68 70	41 50	20 00	126 67	226 35	36 86	23 14	408 25	343 66	209 17	80 48	56 32	25 11
<b>LM75 × LM26</b>	87 55	61 50	40 00	18 25	130 00	75 45	20 78	40 24	329 15	175 28	152 45	50 93	49 44	37 71
<b>LM75 × LM47</b>	96 90	85 40	36 50	35 50	200 00	377 26	29 22	168 00	496 37	694 01	228 33	127 14	48 88	24 17
<b>LM75 × LM48</b>	92 40	439 80	41 17	30 75	160 00	295 52	50 78	54 32	525 67	402 37	269 13	44 89	56 67	12 90
<b>LM75 × LM70</b>	101 90	75 00	46 33	23 25	125 00	220 07	10 98	24 14	363 16	379 13	194 17	115 31	55 13	32 48
<b>LM75 × LM71</b>	85 60	82 50	30 67	34 25	163 33	440 13	25 10	97 58	282 03	617 46	80 00	68 16	31 14	13 11

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

Appendix 4.1 continued

Genotypes	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Parents</b>														
<b>BW140</b>	81 45	75 65	50 00	26 25	87 50	251 50	21 57	63 38	298 94	432 44	162 28	100 48	58 51	27 23
<b>BW141</b>	81 90	68 00	41 33	26 75	109 17	220 07	24 51	22 13	280 90	435 82	125 83	165 49	49 08	40 00
<b>BW152</b>	76 90	44 00	30 33	21 75	142 50	100 60	28 82	59 35	274 85	213 22	88 48	45 52	35 96	29 58
<b>BW162</b>	88 15	51 95	35 83	11 50	193 33	56 59	42 16	14 08	517 27	146 15	240 83	64 51	50 69	48 85
<b>LM26</b>	78 10	60 00	56 50	26 75	125 83	119 46	26 67	129 78	340 68	382 10	160 83	113 55	51 22	45 00
<b>LM47</b>	92 65	50 00	35 33	13 50	120 00	182 34	20 00	45 27	288 20	287 49	126 67	51 18	47 23	21 13
<b>LM48</b>	80 10	54 40	40 50	19 50	87 50	125 75	27 65	101 61	282 40	294 75	142 95	57 59	56 11	29 82
<b>LM70</b>	88 50	81 45	41 00	31 50	170 00	320 67	27 45	57 34	359 30	493 95	138 33	99 09	41 68	22 70
<b>LM71</b>	86 65	68 35	34 50	19 50	135 83	125 75	22 94	34 20	354 36	200 42	167 17	34 58	50 44	20 80
<b>LM75</b>	92 55	85 50	47 67	32 25	242 50	352 11	51 96	88 53	560 51	600 12	248 33	136 32	48 83	26 65
<b>Mean</b>	89 39	73 32	39 85	24 87	150 48	224 89	29 83	59 24	391 10	399 75	178 99	101 21	48 52	34 03
<b>LSD (5%)</b>	13 49	13 49	11 27	11 27	142 30	142 30	33 76	33 76	250 60	250 60	95 90	95 90	8 40	8 40
<b>SEM</b>	0 71	0 71	0 48	0 48	5 52	5 52	1 51	1 51	9 04	9 04	3 37	3 37	0 66	0 66
<b>CV (%)</b>	8 85	8 85	14 71	14 71	29 59	29 59	39 55	39 55	23 50	23 50	23 87	23 87	29 44	29 44

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse, LSD = least significant difference, SEM = standard error of mean, CV = coefficient of variance

Appendix 4.2. Mean values for yield components and biomass traits of 10 bread wheat parental lines, 45 direct crosses and 45 reciprocal crosses evaluated at two sites under non-stressed conditions

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Direct crosses</b>														
<b>BW140 × BW141</b>	87.60	62.20	41.17	20.25	151.67	182.34	14.90	23.14	383.41	538.14	191.70	284.33	52.02	55.21
<b>BW140 × BW152</b>	91.65	78.35	52.33	20.50	119.17	477.86	22.35	35.21	455.45	594.12	268.32	259.30	61.95	46.39
<b>BW140 × BW162</b>	113.20	70.45	38.67	30.00	168.33	282.94	59.22	28.17	535.65	733.37	263.33	360.91	55.27	51.18
<b>BW140 × LM26</b>	102.40	69.25	38.83	32.25	271.67	295.52	46.08	16.10	710.36	629.86	335.57	272.00	50.52	44.32
<b>BW140 × LM47</b>	108.05	75.70	47.17	18.75	130.00	238.93	30.59	63.38	411.40	700.74	214.37	340.54	56.29	53.43
<b>BW140 × LM48</b>	88.75	64.05	46.50	11.00	143.33	81.74	11.37	5.03	516.93	158.86	241.75	61.62	47.82	40.06
<b>BW140 × LM70</b>	94.75	64.25	51.17	27.75	199.17	257.79	27.06	30.18	523.93	557.96	254.45	230.76	51.21	43.72
<b>BW140 × LM71</b>	87.75	69.75	55.50	27.25	159.17	182.34	5.88	20.12	429.86	456.70	226.33	217.30	53.38	49.77
<b>BW140 × LM75</b>	95.45	75.65	43.00	20.25	258.33	465.28	59.61	77.46	719.31	1116.25	343.05	445.54	52.00	42.89
<b>BW141 × BW152</b>	98.10	100.70	45.50	31.75	181.67	528.16	29.80	46.28	492.27	981.84	240.00	348.21	51.90	37.22
<b>BW141 × BW162</b>	92.05	79.40	47.50	33.75	153.33	220.07	24.90	26.16	473.11	578.29	252.03	283.82	56.23	51.40
<b>BW141 × LM26</b>	105.65	73.20	52.83	20.25	318.33	358.39	47.84	39.23	531.16	720.43	-	275.90	-	40.50
<b>BW141 × LM47</b>	108.05	88.75	47.00	19.00	200.83	272.88	29.80	34.20	537.47	658.58	262.25	300.42	51.66	48.11
<b>BW141 × LM48</b>	102.75	65.50	55.50	27.50	163.33	295.52	18.43	28.17	506.24	1039.26	277.33	515.08	56.85	50.94
<b>BW141 × LM70</b>	103.85	88.90	44.17	33.50	248.33	503.01	27.25	17.10	647.55	996.52	317.92	407.19	51.25	41.57
<b>BW141 × LM71</b>	106.05	62.30	44.33	17.75	240.83	106.89	29.02	12.07	660.34	194.44	333.75	64.51	52.87	35.37
<b>BW141 × LM75</b>	103.65	87.20	52.83	34.25	195.00	414.98	20.39	19.11	638.00	546.55	361.20	134.81	58.48	25.56
<b>BW152 × BW162</b>	94.40	67.30	46.83	29.50	176.67	163.48	15.88	20.12	564.08	336.76	317.55	130.91	57.93	41.34
<b>BW152 × LM26</b>	99.35	63.80	36.67	24.00	250.83	138.33	34.12	12.07	619.28	328.57	285.75	152.29	48.83	48.12
<b>BW152 × LM47</b>	100.35	79.10	55.00	27.75	224.17	314.38	30.39	17.10	572.97	597.35	272.15	227.23	50.16	39.16
<b>BW152 × LM48</b>	102.00	80.00	57.17	43.50	170.83	364.68	20.59	25.15	500.42	883.75	264.10	422.15	55.04	49.17
<b>BW152 × LM70</b>	97.95	90.50	50.17	30.75	213.33	320.67	26.27	82.49	610.38	734.94	316.90	283.57	54.25	43.46
<b>BW152 × LM71</b>	102.15	65.75	44.17	19.00	190.00	113.18	41.76	44.26	624.10	439.03	335.33	116.70	57.58	29.56
<b>BW152 × LM75</b>	102.70	75.85	45.83	35.50	303.33	301.80	55.88	33.20	774.57	899.25	355.00	482.26	49.40	55.69
<b>BW162 × LM26</b>	98.35	68.55	56.00	28.75	254.17	226.35	28.82	47.28	672.21	416.94	332.67	122.48	51.71	33.13
<b>BW162 × LM47</b>	104.40	64.60	46.83	24.00	195.83	257.79	46.67	21.13	518.82	588.77	-	264.83	-	46.65
<b>BW162 × LM48</b>	96.60	73.45	58.50	37.00	201.67	339.53	22.55	47.28	560.94	733.89	287.80	296.65	53.46	43.21
<b>BW162 × LM70</b>	96.45	48.25	39.50	10.50	154.17	50.30	22.16	5.03	453.75	87.99	237.12	-	54.94	-
<b>BW162 × LM71</b>	93.05	87.85	41.50	35.00	196.67	471.57	25.69	26.16	650.28	1126.74	365.75	566.64	58.56	51.49
<b>BW162 × LM75</b>	98.90	90.80	52.33	27.00	220.00	427.56	28.04	46.28	637.90	890.80	333.22	539.10	54.64	63.84
<b>LM26 × LM47</b>	107.00	79.30	54.50	30.75	298.33	345.82	60.59	14.08	793.11	743.32	371.10	327.71	50.66	44.94
<b>LM26 × LM48</b>	97.85	72.30	52.67	35.50	174.17	295.52	27.65	32.19	604.98	779.25	344.58	385.93	59.69	51.66
<b>LM26 × LM70</b>	93.70	91.85	45.33	17.00	199.17	540.73	15.69	48.29	579.91	715.62	312.02	152.91	55.30	22.91
<b>LM26 × LM71</b>	102.25	84.00	52.50	21.00	255.00	358.39	48.24	34.20	678.82	772.82	321.02	-	50.91	-
<b>LM26 × LM75</b>	98.00	84.80	43.83	31.00	192.50	509.30	40.00	40.24	644.36	1263.71	352.02	610.40	58.25	49.89
<b>LM47 × LM48</b>	98.35	80.25	58.83	27.50	150.83	345.82	25.69	26.16	509.97	663.00	285.00	248.74	58.85	39.06
<b>LM47 × LM70</b>	102.90	68.95	43.17	13.50	230.83	132.04	35.69	13.08	608.34	216.18	292.15	60.74	51.02	29.91
<b>LM47 × LM71</b>	110.25	76.85	47.33	27.50	291.67	264.08	32.75	23.14	829.27	601.49	431.50	268.61	54.17	46.44
<b>LM47 × LM75</b>	104.50	79.60	38.67	31.00	210.00	276.65	15.29	43.26	449.54	727.61	191.67	348.46	44.14	50.92
<b>LM48 × LM70</b>	92.05	85.45	44.50	34.50	140.00	534.45	15.69	21.13	541.28	1059.05	329.57	430.32	62.70	41.46
<b>LM48 × LM71</b>	101.75	77.25	63.00	49.25	212.50	440.13	52.75	20.12	641.73	1152.50	321.78	591.66	54.63	52.25
<b>LM48 × LM75</b>	97.15	81.55	57.50	35.50	129.17	421.27	28.24	23.14	462.89	1068.53	261.10	533.44	60.07	51.03
<b>LM70 × LM71</b>	101.75	62.00	54.33	26.50	165.83	226.35	20.20	25.15	453.18	661.39	228.33	344.31	52.73	54.12
<b>LM70 × LM75</b>	108.35	86.50	48.17	28.00	239.17	503.01	37.25	57.34	679.43	1215.52	344.45	559.97	53.64	48.35
<b>LM71 × LM75</b>	98.85	73.45	53.83	24.75	261.67	565.88	59.61	27.16	808.99	1229.09	416.85	543.63	55.63	45.23

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

Appendix 4.2. continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Reciprocal crosses</b>														
<b>BW141 × BW140</b>	90 25	64 95	39 50	21 75	110 00	220 07	11 96	37 22	398 00	527 27	235 93	230 76	61 12	47 09
<b>BW152 × BW140</b>	97 20	74 95	51 00	41 75	200 00	377 26	17 45	29 17	559 29	900 93	292 17	422 65	53 92	48 48
<b>BW152 × BW141</b>	108 45	64 65	51 00	23 50	200 83	94 31	42 16	14 08	617 20	307 93	319 83	127 76	55 62	43 48
<b>BW162 × BW140</b>	93 15	58 65	45 83	22 00	160 00	176 05	26 08	6 04	546 61	411 46	308 15	196 05	59 20	48 36
<b>BW162 × BW141</b>	107 00	83 45	48 50	29 25	180 00	352 11	33 73	117 70	595 09	957 99	325 95	417 25	58 06	49 66
<b>BW162 × BW152</b>	97 15	84 05	44 33	31 50	227 50	257 79	30 78	76 46	609 87	679 27	300 50	294 89	51 89	48 92
<b>LM26 × BW140</b>	93 10	68 65	48 17	26 50	145 83	320 67	28 24	26 16	482 46	663 45	263 58	270 62	58 03	42 46
<b>LM26 × BW141</b>	94 60	86 20	56 00	27 50	158 33	276 65	27 61	48 29	536 32	788 11	299 47	395 87	58 87	53 51
<b>LM26 × BW152</b>	100 10	82 10	48 83	48 25	138 33	559 60	46 67	43 26	487 06	1333 06	258 17	624 11	58 62	48 39
<b>LM26 × BW162</b>	95 40	80 75	54 50	33 00	170 83	358 39	32 94	36 22	547 74	926 78	293 98	454 85	57 11	51 07
<b>LM47 × BW140</b>	102 85	70 25	43 67	24 50	159 17	264 08	27 45	21 13	487 56	677 01	257 22	334 88	55 90	51 06
<b>LM47 × BW141</b>	113 25	84 25	45 50	28 50	249 17	257 79	39 41	23 14	641 76	548 85	301 87	228 99	50 12	43 56
<b>LM47 × BW152</b>	87 00	79 60	51 33	20 25	113 33	270 37	13 73	13 08	366 36	519 21	210 40	207 74	59 67	41 04
<b>LM47 × BW162</b>	101 75	72 95	47 67	26 75	195 83	213 78	25 88	56 34	521 33	498 90	256 08	195 54	51 69	44 18
<b>LM47 × LM26</b>	106 20	74 75	53 17	17 00	243 33	320 67	35 29	67 40	804 19	-	449 20	-	58 42	-
<b>LM48 × BW140</b>	91 55	79 60	52 33	44 50	197 50	540 73	17 25	79 48	604 23	1320 84	332 88	598 83	56 71	48 24
<b>LM48 × BW141</b>	102 00	75 25	53 00	19 75	173 33	402 41	39 22	40 24	537 75	666 43	277 95	191 27	55 75	30 55
<b>LM48 × BW152</b>	88 35	79 25	49 50	30 25	141 67	207 49	18 04	83 50	472 84	619 83	267 63	281 06	58 85	52 40
<b>LM48 × BW162</b>	98 80	-	58 00	0 00	213 33	427 56	20 00	2 01	590 89	-	305 60	-	53 53	-
<b>LM48 × LM26</b>	90 50	434 50	59 00	43 50	163 33	282 94	20 00	32 19	577 41	770 06	336 82	388 83	60 43	52 70
<b>LM48 × LM47</b>	109 80	82 85	46 17	27 50	159 17	440 13	20 39	33 20	519 44	618 95	290 50	125 75	58 21	21 47
<b>LM70 × BW140</b>	94 35	77 65	49 83	17 00	150 00	163 48	12 75	77 46	840 12	443 98	274 92	173 54	33 23	47 35
<b>LM70 × BW141</b>	106 60	74 30	51 67	38 75	147 50	169 77	26 27	29 17	700 18	469 36	-	231 13	-	52 51
<b>LM70 × BW152</b>	103 05	87 85	47 00	38 25	195 00	421 27	15 29	15 09	504 55	962 35	251 50	449 56	51 40	47 46
<b>LM70 × BW162</b>	91 40	77 75	47 17	25 50	127 50	301 80	20 98	31 19	450 87	502 47	258 45	152 16	60 12	32 29
<b>LM70 × LM26</b>	96 35	74 85	48 17	21 75	231 67	163 48	21 57	10 06	634 23	248 72	325 63	64 26	53 15	26 93
<b>LM70 × LM47</b>	108 40	84 15	54 83	32 50	141 67	408 69	95 10	36 22	518 75	1038 43	241 02	507 28	56 89	50 62
<b>LM70 × LM48</b>	93 90	-	53 67	-	180 83	-	18 04	2 01	516 84	-	271 77	-	54 48	-
<b>LM71 × BW140</b>	93 10	58 45	57 17	19 00	175 83	484 15	24 71	44 26	494 76	903 68	251 47	339 66	53 50	39 52
<b>LM71 × BW141</b>	103 75	44 25	50 67	21 50	149 17	176 05	25 10	21 13	496 54	459 95	275 45	224 59	58 43	51 18
<b>LM71 × BW152</b>	98 10	55 45	42 50	17 00	117 50	440 13	14 31	28 17	396 19	1022 06	225 97	229 25	59 17	23 07
<b>LM71 × BW162</b>	99 15	78 35	44 00	27 50	340 83	408 69	45 10	18 11	947 08	714 00	479 62	245 47	53 17	35 27
<b>LM71 × LM26</b>	90 40	87 00	43 17	27 25	161 67	616 19	27 25	56 34	511 22	1515 43	275 47	720 43	56 92	49 38
<b>LM71 × LM47</b>	98 50	79 35	54 50	37 25	186 67	301 80	24 90	28 17	570 23	495 98	306 55	217 55	56 21	46 50
<b>LM71 × LM48</b>	102 35	82 60	46 83	32 75	158 33	484 15	27 84	89 54	545 46	1103 35	307 08	452 71	59 33	44 65
<b>LM71 × LM70</b>	96 85	52 40	40 83	16 25	175 83	100 60	25 49	11 07	602 85	29 59	343 18	-	59 44	-
<b>LM75 × BW140</b>	97 60	74 60	47 33	30 50	192 50	333 24	42 75	18 11	615 22	755 81	324 77	345 69	56 73	46 86
<b>LM75 × BW141</b>	95 60	76 85	51 17	32 75	148 33	314 38	29 41	37 22	446 18	892 45	229 43	462 26	55 05	54 05
<b>LM75 × BW152</b>	107 45	79 20	47 33	36 50	226 67	301 80	33 73	30 18	670 40	866 95	350 43	457 23	55 04	54 64
<b>LM75 × BW162</b>	100 00	78 80	50 00	18 75	205 83	396 12	23 92	42 25	622 70	780 45	335 85	292 37	56 09	39 61
<b>LM75 × LM26</b>	102 80	76 15	58 17	26 00	209 17	339 53	22 16	30 18	582 87	945 28	300 47	491 94	53 59	53 76
<b>LM75 × LM47</b>	110 00	81 50	53 50	21 00	198 33	257 79	29 02	27 16	650 91	573 77	362 02	246 85	58 21	45 16
<b>LM75 × LM48</b>	94 10	72 50	46 17	26 00	177 50	389 83	19 22	29 17	578 19	504 67	326 05	239 81	58 33	50 43
<b>LM75 × LM70</b>	90 90	92 10	46 17	30 75	124 17	333 24	22 16	34 20	310 16	746 90	140 03	324 31	48 62	45 50
<b>LM75 × LM71</b>	95 60	73 45	59 83	28 00	219 17	427 56	38 43	54 32	677 24	850 15	358 67	314 76	56 15	39 55

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

Appendix 4.2. continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Parents</b>														
<b>BW140</b>	88 60	69 80	73 83	24 00	222 50	339 53	66 86	25 15	755 84	725 00	398 70	307 97	57 87	44 01
<b>BW141</b>	89 90	59 30	49 50	21 75	190 83	144 61	20 39	10 06	467 65	354 48	219 17	170 77	49 00	49 58
<b>BW152</b>	98 30	79 00	40 67	22 25	175 83	622 47	21 76	40 24	483 57	1361 29	244 42	597 07	52 93	45 20
<b>BW162</b>	99 05	87 20	50 00	27 75	169 17	446 42	31 37	22 13	616 67	927 30	355 67	392 09	60 77	43 32
<b>LM26</b>	87 85	79 95	56 17	33 00	205 00	377 26	22 35	12 07	595 20	753 03	314 40	310 86	54 88	41 95
<b>LM47</b>	104 40	75 85	43 67	25 00	190 00	352 11	14 51	31 19	551 84	762 59	296 87	324 19	55 25	44 32
<b>LM48</b>	86 75	78 05	54 50	22 75	125 00	182 34	19 41	8 05	414 49	455 22	230 83	226 35	58 43	50 62
<b>LM70</b>	94 75	87 40	49 17	39 25	220 83	509 30	23 14	15 09	579 92	1116 00	287 13	505 65	51 57	45 93
<b>LM71</b>	95 55	51 20	40 00	14 00	276 67	157 19	45 88	26 16	584 20	611 20	223 63	276 91	41 54	47 33
<b>LM75</b>	101 85	83 30	42 33	28 75	133 33	345 82	56 67	43 26	595 99	768 82	347 00	324 57	64 34	44 73
<b>Mean</b>	98 77	79 26	49 31	27 27	191 57	325 71	30 01	33 18	572 50	727 14	299 66	511 52	55 23	46 06
<b>LSD (5%)</b>	13 64	13 64	12 25	12 25	141 90	141 90	31 26	31 26	342 70	342 70	183 10	183 10	8 40	8 40
<b>SEM</b>	0 64	0 64	0 58	0 58	6 97	6 97	1 24	1 24	15 71	15 71	7 87	7 87	0 49	0 49
<b>CV (%)</b>	7 27	7 27	14 96	14 96	27 21	27 21	40 07	40 07	24 41	24 41	25 37	25 37	18 67	18 67

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse, LSD = least significant difference, SEM = standard error of mean, CV = coefficient of variance

Appendix 4.3. Estimates of specific combining ability effects of 45 direct crosses obtained from a 10 × 10 diallel cross of bread wheat and evaluated under drought-stressed and non-stressed conditions at two sites

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>Drought-stress</b>														
<b>BW140 x BW141</b>	-11.90	-3.04	-10.06	1.33	-36.85	-13.74	-9.32	-22.06	-165.00	-23.96	-91.18	1.22	4.83	5.83
<b>BW140 x BW152</b>	2.18	10.16	-15.40	4.20	-40.18	137.16	-14.81	52.38	-159.47	160.41	-92.43	36.05	-10.35	4.39
<b>BW140 x BW162</b>	1.93	2.96	3.60	1.70	-10.18	-1.17	-14.03	1.08	-13.85	3.89	-17.98	-5.51	0.29	0.24
<b>BW140 x LM26</b>	6.70	4.36	-1.40	5.33	37.32	14.55	-0.89	1.08	72.63	30.93	41.32	4.17	-2.89	-2.12
<b>BW140 x LM47</b>	1.00	15.16	-6.73	7.33	-3.93	152.88	14.11	31.76	-56.97	233.96	-47.02	15.93	2.57	-13.62
<b>BW140 x LM48</b>	4.75	-1.96	5.27	1.70	31.07	-48.33	-3.14	-20.05	46.09	-99.56	25.91	-35.57	0.30	3.11
<b>BW140 x LM70</b>	10.93	8.89	-4.40	3.83	-31.85	27.13	1.37	-15.52	-55.31	-1.49	-10.84	-20.10	-6.47	-2.45
<b>BW140 x LM71</b>	2.00	7.46	5.19	8.08	2.73	61.71	-2.95	-14.01	32.76	21.53	38.56	10.46	-7.42	-10.16
<b>BW140 x LM75</b>	8.90	-1.49	-3.40	-2.67	69.40	-7.46	21.86	-22.56	126.48	-75.04	40.48	-47.39	-1.72	-11.11
<b>BW141 x BW152</b>	12.06	10.12	-0.56	3.98	21.48	97.55	12.84	27.94	128.25	78.40	70.49	-28.66	-8.86	-10.79
<b>BW141 x BW162</b>	3.98	5.22	-3.81	0.51	-6.43	18.95	6.66	11.84	2.07	-39.24	-8.22	-48.28	3.21	-13.98
<b>BW141 x LM26</b>	7.18	-4.35	13.52	0.13	31.90	-31.35	10.97	-8.78	46.93	-74.41	66.06	-17.72	-6.45	2.61
<b>BW141 x LM47</b>	8.58	-2.08	-8.23	1.76	22.73	-59.64	-1.97	42.02	35.30	-113.77	2.63	-70.60	-9.69	-4.16
<b>BW141 x LM48</b>	-3.82	-1.85	4.43	-3.99	-2.68	-21.92	-7.46	-8.28	-7.69	-64.56	-7.70	-25.96	2.12	0.26
<b>BW141 x LM70</b>	5.76	24.40	4.85	7.13	33.98	191.86	-4.22	1.78	75.11	214.53	28.96	29.44	10.56	-5.11
<b>BW141 x LM71</b>	1.61	-4.13	-0.90	-7.37	-14.35	-50.21	3.23	9.33	33.51	-125.49	6.10	-60.73	3.11	-8.98
<b>BW141 x LM75</b>	6.51	15.47	-4.65	7.88	33.57	66.11	-5.89	25.42	77.53	107.42	32.81	25.16	-1.10	-4.89
<b>BW152 x BW162</b>	-3.23	-0.89	3.09	-3.32	-1.85	-11.23	-0.52	-23.07	4.26	-33.50	8.60	-17.62	-10.71	6.16
<b>BW152 x LM26</b>	0.52	-3.71	4.75	-3.69	10.65	-102.40	1.74	-15.02	47.78	-84.93	33.18	-12.65	-4.78	4.73
<b>BW152 x LM47</b>	7.84	3.31	9.59	1.68	61.90	-1.80	17.43	-0.43	136.92	44.75	52.16	-0.27	-2.43	-3.20
<b>BW152 x LM48</b>	2.34	8.99	0.50	7.93	-56.02	45.36	-14.63	14.16	-111.31	157.27	-31.82	33.62	0.29	-1.11
<b>BW152 x LM70</b>	-0.43	12.44	-0.25	-1.69	16.90	67.37	-3.65	6.11	56.44	97.25	39.85	5.14	4.96	-9.37
<b>BW152 x LM71</b>	2.57	-0.31	6.92	-2.69	-6.43	-30.09	6.54	-7.98	-20.36	-51.42	-14.56	-6.30	-0.58	-1.42
<b>BW152 x LM75</b>	1.24	7.04	7.25	6.56	11.07	10.78	0.27	0.57	61.84	81.26	46.10	18.47	-4.80	4.16
<b>BW162 x LM26</b>	0.03	8.67	3.07	6.58	40.82	149.10	-0.40	44.54	23.49	223.35	-4.12	51.69	0.12	-7.46
<b>BW162 x LM47</b>	4.11	6.25	-4.68	2.45	3.73	51.65	-6.67	2.28	-93.00	72.90	-66.62	8.37	-1.06	-5.07
<b>BW162 x LM48</b>	-1.24	10.40	2.32	9.20	-34.18	108.24	-0.79	20.90	-49.47	211.22	-2.04	36.10	1.21	-3.84
<b>BW162 x LM70</b>	1.51	4.87	0.57	6.33	-32.93	-30.09	11.27	1.28	-8.26	-40.72	21.80	3.28	-2.64	-1.03
<b>BW162 x LM71</b>	-0.79	-6.00	0.82	-4.42	-17.52	-42.67	-11.28	-19.34	-74.45	-127.28	-42.04	-26.02	-3.06	1.53
<b>BW162 x LM75</b>	9.31	9.67	4.65	5.58	34.98	67.37	2.25	11.34	101.71	87.81	65.46	-0.05	-0.05	-6.10
<b>LM26 x LM47</b>	10.62	5.49	-11.26	1.20	17.07	-13.74	-4.01	-5.56	-17.10	-32.40	-40.02	-13.86	-3.63	-1.43
<b>LM26 x LM48</b>	-0.58	1.54	5.07	2.33	-47.10	55.42	-2.24	3.49	-36.76	54.30	-3.49	-14.87	-9.34	-10.06

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

## Appendix 4.3. continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>LM26 x LM70</b>	2.74	3.32	-3.93	0.20	8.73	86.86	-0.48	-8.08	19.04	114.97	-5.03	-33.73	-4.08	-13.69
<b>LM26 x LM71</b>	-0.86	11.02	-10.43	0.33	-20.85	96.29	2.46	12.55	-22.96	159.91	-18.16	32.73	4.57	-9.80
<b>LM26 x LM75</b>	-0.71	6.77	-10.43	-3.05	-34.60	-7.46	-5.18	8.52	-63.96	-36.29	-34.91	-42.85	4.59	-10.63
<b>LM47 x LM48</b>	-2.79	-0.38	5.24	0.18	-32.27	-26.95	-8.38	-9.99	-0.16	49.55	34.84	11.26	9.01	2.68
<b>LM47 x LM70</b>	-1.32	12.35	2.07	5.05	44.40	57.93	-2.50	-3.95	108.69	51.88	57.32	13.47	1.00	-6.13
<b>LM47 x LM71</b>	-6.69	-0.88	10.49	-5.20	-51.85	17.07	-0.24	-25.08	-52.20	-199.21	0.14	-30.04	-8.86	13.60
<b>LM47 x LM75</b>	-3.34	9.05	-0.43	4.30	8.98	61.08	0.54	-9.49	53.01	102.89	37.40	33.21	0.46	-4.72
<b>LM48 x LM70</b>	2.67	18.69	-11.85	1.80	8.90	-2.02	-0.06	10.18	-20.18	32.45	-29.69	22.77	8.39	0.74
<b>LM48 x LM71</b>	5.04	7.32	-3.93	4.96	5.57	109.86	12.09	42.82	-25.01	142.21	-41.36	-4.75	-0.43	-12.81
<b>LM48 x LM75</b>	2.62	-1.76	1.32	-3.41	58.48	-9.60	7.68	-5.47	125.13	-63.07	71.13	-36.82	-12.12	-7.41
<b>LM70 x LM71</b>	-3.43	-10.37	-2.51	-5.16	-13.60	-23.43	12.07	20.68	-16.74	-35.04	-12.77	-22.13	11.00	2.18
<b>LM70 x LM75</b>	4.74	-3.30	8.82	-1.29	-17.77	-17.15	-16.36	-10.50	-23.22	-29.85	9.56	3.58	3.99	-0.03
<b>LM71 x LM75</b>	0.99	7.56	-3.89	6.40	42.57	84.34	0.48	17.38	27.52	166.03	-5.91	9.96	-11.76	-3.54
<b>Non-stress</b>														
<b>BW140 x BW141</b>	-2.30	-0.08	-10.04	-1.35	-31.27	-77.92	-12.80	-5.45	-76.12	-98.92	-51.64	-24.97	-3.42	2.97
<b>BW140 x BW152</b>	3.20	12.99	1.30	8.78	-2.52	148.44	-6.33	-3.44	40.54	115.90	14.79	58.47	4.02	-0.11
<b>BW140 x BW162</b>	11.95	0.89	-8.12	3.65	2.07	-49.62	16.42	-18.53	74.30	-59.21	20.29	-4.03	3.00	-0.22
<b>BW140 x LM26</b>	6.52	5.29	-6.87	7.03	46.65	28.97	10.93	-14.51	129.58	15.03	34.12	-11.20	0.40	-3.02
<b>BW140 x LM47</b>	14.22	9.32	-4.95	-0.72	-17.52	-27.62	2.79	6.62	-17.35	57.25	-29.66	55.20	1.57	7.47
<b>BW140 x LM48</b>	-1.08	8.17	-0.95	5.40	8.32	32.12	-11.91	6.62	93.75	108.23	21.86	47.71	1.80	-5.86
<b>BW140 x LM70</b>	3.32	7.29	0.13	0.03	12.48	-68.49	-6.33	18.19	3.81	-130.66	-15.81	-80.36	2.18	2.32
<b>BW140 x LM71</b>	-0.80	0.44	5.96	0.78	5.40	54.12	-10.93	-3.44	-4.52	48.56	-26.55	-4.03	-0.47	2.25
<b>BW140 x LM75</b>	5.30	11.47	-5.20	3.03	63.32	120.14	24.95	12.15	200.44	304.40	68.46	113.10	0.39	-0.70
<b>BW141 x BW152</b>	1.14	10.63	-0.12	3.15	7.65	90.97	9.03	-0.02	43.48	109.17	4.96	8.99	0.66	-6.70
<b>BW141 x BW162</b>	-2.61	9.38	-0.37	7.03	-16.93	65.82	2.36	41.73	22.85	232.42	14.04	121.54	3.70	3.71
<b>BW141 x LM26</b>	-2.01	7.65	6.04	-0.60	54.73	97.26	10.78	13.56	22.48	218.55	50.76	106.89	-0.60	0.24
<b>BW141 x LM47</b>	8.51	14.45	-2.12	-0.72	41.40	45.07	7.66	-1.53	78.36	68.00	7.11	35.72	-2.69	2.03
<b>BW141 x LM48</b>	0.24	-1.67	5.88	-0.85	-15.27	128.69	1.87	4.00	10.74	317.13	2.69	124.18	2.84	-2.04
<b>BW141 x LM70</b>	3.09	9.55	-0.45	11.65	14.32	116.12	-0.18	-7.06	162.61	197.22	108.96	90.17	4.16	3.36
<b>BW141 x LM71</b>	2.76	-18.77	-0.87	-4.85	11.40	-78.80	0.11	-13.60	67.19	-208.52	29.65	-84.44	2.31	-5.83
<b>BW141 x LM75</b>	-2.51	9.98	3.63	9.03	-11.93	144.41	-2.05	-2.03	30.83	183.78	20.36	69.54	3.26	-6.68
<b>BW152 x BW162</b>	-2.67	-2.93	0.11	-0.90	19.40	-155.88	-3.09	8.53	66.67	-342.54	46.25	-140.63	1.14	-2.48

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass, (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>) and GY = grain yield (g m<sup>-2</sup>), HI = harvest index (%), GH = greenhouse

## Appendix 4.3. continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>BW152 x LM26</b>	1.28	-5.65	-2.72	4.73	11.90	-17.56	13.97	-12.09	32.86	-19.74	9.18	34.67	-0.99	1.78
<b>BW152 x LM47</b>	-4.77	0.75	7.69	-7.40	-13.93	-74.14	-4.37	-24.67	-50.64	-292.28	-21.50	-136.04	-1.20	-7.83
<b>BW152 x LM48</b>	-3.27	1.02	7.86	5.48	-26.43	-80.43	-7.11	14.57	-33.68	-98.77	3.09	-1.92	3.32	4.39
<b>BW152 x LM70</b>	2.06	10.57	3.11	3.10	21.48	4.45	-5.64	9.03	37.16	-1.92	21.42	13.04	-0.96	-1.05
<b>BW152 x LM71</b>	1.68	-18.00	-2.14	-13.40	-28.93	-89.86	1.62	-3.54	-10.16	-120.01	17.87	-180.55	4.43	1.99
<b>BW152 x LM75</b>	6.63	-1.08	1.11	4.60	82.32	-64.71	18.38	-8.07	202.17	32.54	89.94	116.22	-2.42	8.68
<b>BW162 x LM26</b>	-1.29	-3.15	7.79	0.89	15.98	5.34	0.13	5.11	-6.09	62.65	-18.73	15.39	-3.16	-2.33
<b>BW162 x LM47</b>	4.91	-9.02	-0.21	-4.61	-0.68	-51.24	5.52	2.09	-51.13	-65.38	-29.85	-43.08	-2.06	-0.98
<b>BW162 x LM48</b>	-0.46	8.23	10.79	15.85	10.98	35.46	-9.48	-11.99	-40.15	6.14	-35.36	2.32	-4.02	1.87
<b>BW162 x LM70</b>	-4.24	-14.80	-4.12	-11.99	-55.68	-110.98	-9.19	-18.53	-163.76	-313.98	-84.27	-169.27	1.43	-3.42
<b>BW162 x LM71</b>	-2.06	5.30	-4.71	1.26	72.23	153.10	4.63	-14.51	182.62	311.16	90.63	132.78	-1.98	-2.66
<b>BW162 x LM75</b>	1.29	7.00	3.71	-7.11	16.40	124.81	-4.78	7.63	14.24	226.41	2.48	142.47	-2.59	6.39
<b>LM26 x LM47</b>	10.40	-2.03	1.68	-5.85	37.73	-49.62	11.25	8.13	145.97	-70.17	65.60	4.95	-0.73	1.54
<b>LM26 x LM48</b>	-2.03	-6.11	3.68	9.78	-64.35	-93.64	-12.87	-0.42	-61.48	-69.28	-3.85	3.88	5.94	9.83
<b>LM26 x LM70</b>	-1.18	4.29	-5.41	-10.35	-17.68	-30.76	-18.07	-3.44	-45.61	-361.76	-25.73	-274.92	-0.88	-18.12
<b>LM26 x LM71</b>	0.12	6.44	-4.32	-5.60	-24.77	104.42	1.05	12.66	-57.65	196.10	-46.31	91.40	0.13	2.99
<b>LM26 x LM75</b>	4.20	1.42	-1.15	-1.22	-32.27	41.55	-5.62	2.60	-39.06	260.56	-18.31	167.67	1.43	8.60
<b>LM47 x LM48</b>	-6.20	2.15	4.19	5.00	-49.35	127.44	-4.74	0.48	-62.91	83.64	-6.69	-50.12	5.89	-11.24
<b>LM47 x LM70</b>	-4.62	-2.85	0.69	0.50	-18.10	4.83	-3.07	-4.55	-47.73	69.97	-27.85	46.64	-1.25	-2.06
<b>LM47 x LM71</b>	-5.90	-1.30	2.61	9.88	34.82	17.40	1.05	-3.54	122.13	-8.60	74.59	5.71	2.56	4.39
<b>LM47 x LM75</b>	-3.02	1.15	-2.22	3.50	-0.18	1.68	-5.62	6.02	-27.39	93.36	-17.59	60.29	-1.98	4.34
<b>LM48 x LM70</b>	-0.47	10.35	-8.39	1.09	21.90	16.81	-0.46	-18.83	33.45	43.44	20.84	19.71	-1.94	2.41
<b>LM48 x LM71</b>	8.61	-1.95	-2.56	1.84	46.90	111.73	22.97	24.43	97.99	333.78	34.61	159.13	-1.99	1.20
<b>LM48 x LM75</b>	2.18	-4.85	-5.64	-8.41	14.82	55.14	6.40	-4.25	24.93	-7.54	13.75	23.57	-0.10	12.29
<b>LM70 x LM71</b>	1.76	-24.91	1.08	-7.35	-8.18	-148.22	6.71	-6.36	9.54	-285.60	11.68	-82.57	2.32	7.55
<b>LM70 x LM75</b>	2.09	7.19	0.66	0.65	2.65	106.43	13.58	21.31	-23.68	350.12	-31.83	181.00	-3.75	3.63
<b>LM71 x LM75</b>	-1.28	12.20	8.55	4.13	10.82	171.70	11.79	10.34	-65.88	287.78	61.90	121.39	2.48	-5.74

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index, GH = greenhouse

Appendix 4.4. Estimates of reciprocal effects of 45 reciprocal crosses obtained from a 10 × 10 diallel cross of bread wheat and evaluated under drought-stressed and non-stressed conditions at two different sites

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
	<b>Drought-stress</b>													
<b>BW140 x BW141</b>	1.10	4.50	-7.42	0.13	25.83	-22.01	6.27	1.01	-10.30	-19.60	-36.25	1.19	4.83	4.83
<b>BW140 x BW152</b>	-7.53	1.25	-4.08	-2.75	-20.83	-53.44	2.35	-12.07	-48.50	3.64	-39.17	-10.75	-10.35	-10.35
<b>BW140 x BW162</b>	1.58	-2.70	-3.92	-2.00	39.17	15.72	4.71	28.17	102.66	47.86	13.04	3.40	0.29	0.29
<b>BW140 x LM26</b>	4.20	-7.45	6.75	0.38	24.17	25.15	6.67	24.14	145.40	65.92	97.92	14.21	-2.89	-2.89
<b>BW140 x LM47</b>	5.05	-5.20	8.42	-0.63	22.92	-37.73	6.57	-20.62	75.80	-28.16	39.58	8.49	2.57	2.57
<b>BW140 x LM48</b>	4.00	-5.13	-0.42	0.25	24.58	6.29	7.55	2.01	67.24	20.66	30.01	10.56	0.30	0.30
<b>BW140 x LM70</b>	-2.43	3.63	-3.59	-3.88	-13.33	18.86	-21.08	-9.56	-49.55	12.54	-12.94	2.77	-6.47	-6.47
<b>BW140 x LM71</b>	-1.45	0.55	-7.67	2.38	-51.25	97.46	-8.92	5.03	-96.06	120.27	-30.68	-26.53	-7.42	-7.42
<b>BW140 x LM75</b>	2.10	4.50	-4.42	1.38	-28.75	40.87	6.67	9.56	-45.00	72.64	-19.58	18.99	-1.72	-1.72
<b>BW141 x BW152</b>	-3.05	5.93	-4.00	3.40	-32.50	122.61	6.37	24.65	-9.39	159.69	14.31	10.63	-8.86	-8.86
<b>BW141 x BW162</b>	1.23	14.68	0.25	5.63	-10.42	37.73	-12.94	22.64	-19.83	101.04	3.02	34.77	3.21	3.21
<b>BW141 x LM26</b>	-11.48	7.20	-0.92	2.00	-102.92	75.45	-29.22	12.07	-107.11	131.74	-51.00	37.79	-6.45	-6.45
<b>BW141 x LM47</b>	-2.33	10.83	-6.00	5.13	-16.25	91.17	0.39	47.79	-38.67	164.41	-19.50	21.76	-9.69	-9.69
<b>BW141 x LM48</b>	-0.18	1.25	4.50	1.13	50.83	-34.58	5.49	0.50	111.90	-87.48	47.50	-37.47	2.12	2.12
<b>BW141 x LM70</b>	-0.60	-6.85	3.58	2.00	33.33	-204.35	0.10	5.53	60.73	-181.23	23.33	15.03	10.56	10.56
<b>BW141 x LM71</b>	1.00	11.13	-2.83	3.75	1.67	62.88	-13.43	34.20	-88.08	151.15	-42.97	46.21	3.11	3.11
<b>BW141 x LM75</b>	-3.50	-4.13	1.75	0.75	-17.08	22.01	-11.18	-9.05	-16.19	18.32	10.32	4.59	-1.10	-1.10
<b>BW152 x BW162</b>	-3.90	10.98	-5.34	8.25	47.08	66.02	2.25	18.11	30.81	189.82	-15.83	28.67	-10.71	-10.71
<b>BW152 x LM26</b>	-5.35	9.20	-7.50	7.63	-29.58	75.45	-4.71	4.02	-125.45	114.71	-77.92	30.12	-4.78	-4.78
<b>BW152 x LM47</b>	2.63	12.48	6.34	4.75	83.33	69.16	17.06	0.50	187.88	100.27	74.78	26.16	-2.43	-2.43
<b>BW152 x LM48</b>	3.43	2.10	-5.92	-3.50	0.42	22.01	4.80	-9.05	-5.02	21.65	-8.75	-2.07	0.29	0.29
<b>BW152 x LM70</b>	3.05	-3.05	7.67	-0.63	11.67	-81.74	6.37	-1.01	138.45	-53.07	102.92	0.13	4.96	4.96
<b>BW152 x LM71</b>	3.05	-9.80	0.33	-6.13	40.83	-66.02	15.00	-31.19	143.38	-209.32	74.83	-50.30	-0.58	-0.58
<b>BW152 x LM75</b>	-6.98	6.05	0.67	1.63	-48.33	37.73	-6.18	14.59	-100.33	91.57	-39.17	32.70	-4.80	-4.80
<b>BW162 x LM26</b>	-4.10	-2.58	0.92	-1.00	44.17	-15.72	15.59	-39.23	69.50	-43.78	8.33	-24.58	0.12	0.12
<b>BW162 x LM47</b>	2.83	-1.10	1.83	-1.63	2.08	-31.44	-1.47	-1.01	10.36	-55.54	8.33	-19.74	-1.06	-1.06
<b>BW162 x LM48</b>	1.63	0.95	2.34	-3.13	-5.00	-31.44	-5.78	-6.54	1.40	-8.25	10.42	-0.82	1.21	1.21
<b>BW162 x LM70</b>	-4.03	0.53	0.09	2.00	-10.42	94.31	7.65	6.04	52.87	149.17	47.56	20.43	-2.64	-2.64
<b>BW162 x LM71</b>	-2.68	12.60	-1.67	6.00	-16.67	75.45	1.96	18.61	-8.33	79.42	-7.92	25.09	-3.06	-3.06
<b>BW162 x LM75</b>	-2.18	-8.63	1.50	-9.00	-47.50	-28.29	3.14	-37.22	-77.03	-84.50	-27.92	-16.22	-0.05	-0.05
<b>LM26 x LM47</b>	3.33	-2.25	2.67	0.50	10.83	15.72	-8.92	6.54	-0.85	20.70	-2.36	6.92	-3.63	-3.63
<b>LM26 x LM48</b>	-3.73	0.85	-7.50	-0.13	-5.83	103.75	-3.63	20.62	-14.35	123.93	-4.18	-0.38	-9.34	-9.34

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index, GH = greenhouse

## Appendix 4.4 continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>LM26 x LM70</b>	0.35	-4.23	0.33	2.75	47.50	9.43	13.63	23.14	80.94	43.54	16.93	9.81	-4.08	-4.08
<b>LM26 x LM71</b>	-5.95	-2.88	-3.00	-0.63	-32.08	0.00	-4.22	9.56	-84.90	51.56	-41.54	35.90	4.57	4.57
<b>LM26 x LM75</b>	-2.05	-10.38	1.83	-6.25	1.67	-110.03	-5.20	-17.61	-12.67	-165.08	-7.81	-32.00	4.59	4.59
<b>LM47 x LM48</b>	-4.58	-8.45	-5.75	-1.13	-10.83	-119.46	6.96	-9.05	-14.78	-196.08	-9.33	-11.63	9.01	9.01
<b>LM47 x LM70</b>	3.05	3.93	-0.58	3.75	5.83	34.58	7.75	-9.05	10.82	-5.21	-2.36	5.53	1.00	1.00
<b>LM47 x LM71</b>	1.43	5.50	4.50	-0.50	1.25	-62.88	4.51	-10.06	40.31	-90.00	29.53	-4.40	-8.86	-8.86
<b>LM47 x LM75</b>	3.03	6.08	2.42	7.50	7.08	69.16	-2.16	12.58	44.64	93.51	33.94	15.97	0.46	0.46
<b>LM48 x LM70</b>	2.20	3.78	-7.75	-5.79	21.25	-74.16	0.39	-39.68	8.48	-107.10	-11.25	3.57	8.39	8.39
<b>LM48 x LM71</b>	8.53	-0.20	3.50	1.13	-25.42	0.00	-6.08	-36.22	-28.08	-43.79	2.92	-6.48	-0.43	-0.43
<b>LM48 x LM75</b>	3.35	13.18	-3.42	6.50	3.33	100.60	21.08	13.08	101.65	103.60	40.40	-8.61	-12.12	-12.12
<b>LM70 x LM71</b>	0.48	-11.78	-4.25	-5.00	-22.92	-119.46	-9.41	-13.58	-32.86	-137.39	-0.46	-3.71	11.00	11.00
<b>LM70 x LM75</b>	3.20	-9.65	-0.92	-5.63	-11.25	-81.74	0.59	-12.58	-9.78	-91.67	0.75	2.26	3.99	3.99
<b>LM71 x LM75</b>	-3.20	5.18	-4.33	6.00	-2.08	119.46	-7.25	30.18	-77.04	137.36	-57.87	-10.50	-11.76	-11.76
<b>Non-stress</b>														
<b>BW140 x BW141</b>	1.33	1.38	-0.84	0.75	-20.83	18.86	-1.47	7.04	7.30	-5.43	22.12	-26.79	10.14	-4.75
<b>BW140 x BW152</b>	2.78	-1.70	-0.67	10.63	40.42	-50.30	-2.45	-3.02	51.92	153.41	11.93	81.68	-4.03	1.91
<b>BW140 x BW162</b>	-10.03	-5.90	3.58	-4.00	-4.17	-53.44	-16.57	-11.07	5.48	-160.95	22.41	-82.43	1.67	-5.40
<b>BW140 x LM26</b>	-4.65	-0.30	4.67	-2.88	-62.92	12.58	-8.92	5.03	-113.95	16.80	-35.99	-0.69	3.92	-1.17
<b>BW140 x LM47</b>	-2.60	-2.73	-1.75	2.88	14.58	12.58	-1.57	-21.13	38.08	-11.86	21.43	-2.83	0.38	-5.21
<b>BW140 x LM48</b>	1.40	7.78	2.92	16.75	27.08	229.50	2.94	37.22	43.65	580.99	45.57	268.61	0.98	7.50
<b>BW140 x LM70</b>	-0.20	6.70	-0.67	-5.38	-24.58	-47.16	-7.16	23.64	-53.30	-56.99	-4.81	-28.61	5.38	4.78
<b>BW140 x LM71</b>	2.68	-5.65	0.83	-4.13	8.33	150.90	9.41	12.07	32.45	223.49	12.57	61.18	0.04	-0.24
<b>BW140 x LM75</b>	1.08	-0.53	2.17	5.13	-32.92	-66.02	-8.43	-29.68	-52.04	-180.22	-9.14	-49.92	2.42	-0.44
<b>BW141 x BW152</b>	5.18	-18.03	2.75	-4.13	9.58	-216.92	6.18	-16.10	62.46	-336.95	39.92	-110.22	2.34	3.97
<b>BW141 x BW162</b>	7.48	2.03	0.50	-2.25	13.33	66.02	4.41	45.77	60.99	189.85	36.96	66.71	0.62	-1.14
<b>BW141 x LM26</b>	-5.53	6.50	1.58	3.63	-80.00	-40.87	-10.12	4.53	2.58	33.84	-26.24	59.98	9.09	6.27
<b>BW141 x LM47</b>	2.60	-2.25	-0.75	4.75	24.17	-7.55	4.80	-5.53	52.15	-54.86	19.81	-35.71	-0.78	-5.65
<b>BW141 x LM48</b>	-0.38	4.88	-1.25	-3.88	5.00	53.44	10.39	6.04	15.75	-186.41	0.31	-161.91	-0.29	-6.18
<b>BW141 x LM70</b>	1.38	-7.30	3.75	2.63	-50.42	-166.62	-0.49	6.04	26.31	-263.58	66.00	-88.03	6.46	9.34
<b>BW141 x LM71</b>	-1.15	-9.03	3.17	1.88	-45.83	34.58	-1.96	4.53	-81.90	132.76	-29.15	80.04	2.72	9.45
<b>BW141 x LM75</b>	-4.03	-5.18	-0.84	-0.75	-23.33	-50.30	4.51	9.05	-95.91	172.95	-65.88	163.73	-2.18	14.63
<b>BW152 x BW162</b>	1.38	8.38	-1.25	1.00	25.42	47.16	7.45	28.17	22.89	171.25	-8.53	81.99	-3.21	4.99

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

## Appendix 4.4. continued

Genotype	PH		KPS		SB		RB		PB		GY		HI	
	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH	Field	GH
<b>BW152 x LM26</b>	0.38	9.15	6.09	12.13	-56.25	210.63	6.27	15.59	-66.11	502.24	-13.79	235.91	4.88	0.13
<b>BW152 x LM47</b>	-6.68	0.25	-1.83	-3.75	-55.42	-22.01	-8.33	-2.01	-103.31	-39.07	-30.88	-9.75	1.93	2.45
<b>BW152 x LM48</b>	-6.83	-0.38	-3.83	-6.63	-14.58	-78.60	-1.27	29.17	-13.79	-131.96	1.77	-70.55	2.02	1.82
<b>BW152 x LM70</b>	2.55	-1.33	-1.58	3.75	-9.17	50.30	-5.49	-33.70	-52.92	113.71	-32.70	83.00	-1.19	1.66
<b>BW152 x LM71</b>	-2.03	-5.15	-0.84	-1.00	-36.25	163.48	-13.73	-8.05	-113.95	291.52	-54.68	56.27	0.51	-1.74
<b>BW152 x LM75</b>	2.38	1.68	0.75	0.50	-38.33	0.00	-11.08	-1.51	-52.08	-16.15	-2.28	-12.51	1.90	-0.60
<b>BW162 x LM26</b>	-1.48	6.10	-0.75	2.13	-41.67	66.02	2.06	-5.53	-62.24	254.92	-19.34	166.18	2.80	6.72
<b>BW162 x LM47</b>	-1.33	4.18	0.42	1.38	0.00	-22.01	-10.39	17.61	-43.60	-44.94	-46.13	-34.64	-4.14	-1.70
<b>BW162 x LM48</b>	1.10	12.58	-0.25	8.84	5.83	-17.04	-1.27	-22.64	14.97	-118.53	8.90	-21.06	-0.07	5.07
<b>BW162 x LM70</b>	-2.53	14.75	3.83	7.50	-13.33	125.75	-0.59	13.08	-1.44	207.24	10.67	48.16	4.02	-11.64
<b>BW162 x LM71</b>	3.05	-4.75	1.25	-3.75	72.08	-31.44	9.71	-4.02	148.40	-206.37	56.93	-160.59	-2.17	-8.66
<b>BW162 x LM75</b>	0.55	-6.00	-1.17	-4.13	-7.08	-15.72	-2.06	-2.01	-7.60	-55.18	1.32	-123.36	1.12	-14.76
<b>LM26 x LM47</b>	-0.40	-2.28	-0.67	-6.88	-27.50	-12.58	-12.65	26.66	5.54	30.43	39.05	60.75	2.91	-1.21
<b>LM26 x LM48</b>	-3.68	0.65	3.17	4.00	-5.42	-6.29	-3.82	0.00	-13.78	-4.60	-3.88	1.45	0.28	0.89
<b>LM26 x LM70</b>	1.33	-8.50	1.42	2.38	16.25	-188.63	2.94	-19.11	27.16	-233.45	6.81	-44.33	-0.43	1.95
<b>LM26 x LM71</b>	-5.93	1.50	-4.67	3.13	-46.67	128.90	-10.49	11.07	-83.80	475.40	-22.78	245.53	3.64	2.82
<b>LM26 x LM75</b>	2.40	-4.33	7.17	-2.50	8.33	-84.88	-8.92	-5.03	-30.74	-159.21	-25.78	-59.23	-2.51	1.80
<b>LM47 x LM48</b>	5.73	1.30	-6.34	0.00	4.17	47.16	-2.65	3.52	4.74	-22.02	2.75	-61.49	0.41	-8.74
<b>LM47 x LM70</b>	2.75	7.60	5.84	9.50	-44.58	138.33	-10.98	11.57	-78.45	411.13	-25.57	223.27	0.81	10.58
<b>LM47 x LM71</b>	-5.88	1.25	3.58	4.88	-52.50	18.86	-3.92	2.52	-129.52	-52.75	-62.48	-25.53	0.77	1.48
<b>LM47 x LM75</b>	2.75	0.95	7.42	-5.00	-5.83	-9.43	6.86	-8.05	100.68	-76.92	85.18	-50.80	7.25	-4.85
<b>LM48 x LM70</b>	0.93	6.78	4.58	5.75	20.42	-167.22	1.18	-9.56	-12.22	-221.47	-28.90	-47.56	-3.40	7.61
<b>LM48 x LM71</b>	0.30	2.68	-8.09	-8.25	-27.08	22.01	-12.45	34.71	-48.13	-24.58	-7.35	-69.48	2.00	-4.45
<b>LM48 x LM75</b>	-1.53	-4.53	-5.67	-4.75	24.17	-15.72	-4.51	3.02	57.65	-281.93	32.48	-146.82	-1.14	8.52
<b>LM70 x LM71</b>	-2.45	-4.80	-6.75	-5.13	5.00	-62.88	2.65	-7.04	74.83	-315.90	57.43	-165.74	1.86	-4.11
<b>LM70 x LM75</b>	-8.73	2.80	-1.00	1.38	-57.50	-84.88	-7.55	-11.57	-184.63	-234.31	-102.21	-117.83	-3.26	-1.63
<b>LM71 x LM75</b>	-1.63	0.00	3.00	1.63	-21.25	-69.16	-10.59	13.58	-65.88	-189.47	-29.09	-114.43	-0.57	-1.98

PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass, ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), HI = harvest index (%), GH = greenhouse

## **Chapter 5: Assessing Genetic Variability to Advance Grain Yield, Drought Adaption and Biomass Allocation in Wheat (*Triticum aestivum* L.) Populations**

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### **Abstract**

Selection gains and genetic progress determine breeding success for drought adaptation and climate-smart crop varieties. Quantifying the magnitude of genetic variance components in new breeding populations guides selection for grain yield (GY) and yield components and biomass and root system attributes. Root traits are vital in soil nutrient and water uptake, mobilization, and atmospheric carbon transfer to the plant-soil system. The objective of this study was to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement. One hundred bread wheat genotypes comprising of 10 parental lines and 90 F<sub>2</sub> families developed using a full diallel mating design were evaluated for plant height (PH), kernels per spike (KPS), shoot biomass (SB), root biomass (RB), total plant biomass (PB) and GY at two sites under drought-stressed and non-stressed conditions. Higher phenotypic coefficient of variation (PCV) than genotypic coefficient of variation (GCV) was observed for PH, SB, RB, PB and GY. Heritability and genetic advance as a percentage of the mean (GAM) of 41.61% and 3.49%, respectively, were computed for RB under drought-stressed condition. Based on correlation and principal component analyses, geometric mean productivity (GMP) and stress tolerance index (STI) were prioritised for selecting drought-tolerant families with high RB. Direct crosses such as BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 were identified with better GY under drought conditions and are thus recommended for genetic advancement. Further research should also consider nutrient uptake and transfer of atmospheric carbon to soils for maintaining high GY, soil quality and mitigating climate change.

**Keywords:** *Biomass allocation, Drought tolerance, Genotypic coefficient of variation, Heritability, Root biomass, Wheat*

## 5.1 Introduction

Climate-induced extreme temperatures and unpredictability of rainfall patterns increase the severity of drought in the world's most vulnerable regions. Drought and heat stress remain the most important abiotic stresses affecting wheat growth and development and yield gains (Kang et al., 2019). Bread wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ , AABBDD), a predominantly rainfed crop, has the greatest production area under rainfed farming after maize globally (Zampieri et al., 2017). Erratic rainfall in dryland wheat production areas causes extreme moisture stress at different crop growth stages and leads to high yield variability over space and time (Daryanto et al., 2017). For instance, wheat yield losses in arid and semi-arid regions ranged from over 40% under mild drought stress and up to 92% under severe drought (Li et al., 2021). In a global meta-analysis focusing on rice and wheat, Zhang et al. (2018) reported drought-related wheat yield losses of up to 27.5%. Drought adaptation is a critical mechanism that can be exploited in wheat breeding programs to bolster yield gains and meet global food demand (Iseki et al., 2018). Water is a scarce natural resource, and with added irrigation costs, the use of freshwater for agricultural production is unsound and unsustainable. Hence, breeding for drought tolerance presents the most sustainable strategy for drought adaptation in the arid and semi-arid regions of the world (Pereira et al., 2002; Sambatti et al., 2007; Li et al., 2020).

Breeding for drought tolerance depends on high throughput yield performance evaluation as a basis for selecting superior genotypes (Khadka et al., 2020). However, the genetic control of grain yield under drought is complex, and component traits with high heritability and correlated with yield can be targeted during selection to increase selection response and genetic gain (Dixit et al., 2014). The most influential morphological traits that can be used for drought tolerance screening include reduced plant height, increased tillering capacity, early flowering and maturity times, better spike-related traits and biomass partitioning between shoots and roots (Mwadzingeni et al., 2016; Mathew et al., 2018). The utility of biomass allocation as a target trait in wheat breeding remains unexplored due to the difficulty and time-consuming procedure of root sampling and measurements in field trials and the need for specialised equipment for *in-situ* data acquisition (Voss-Fels et al., 2018). Consequently, breeders have focused crop improvement efforts on above ground yield related traits without any direct selection for root traits (Mathew and Shimelis 2022). Designing new wheat ideotypes with altered biomass allocation along with better conversion efficiency enhances yield gains (Mathew et al., 2019; Shamuyarira et al., 2022). According to

Dolezal et al. (2021), plants adapt to water stress by changing their total biomass or biomass allocation between shoots and roots to optimize growth and development. Enhancing biomass allocation to the root system in wheat can significantly improve grain yield under drought by enhancing exploration for water and nutrients to support aboveground biomass production. Also, biomass is linked with efficient light capture and carbon assimilation (Antar et al., 2021; Bacher et al., 2021; Ma et al., 2021).

Increasing biomass allocation to the roots may provide additional benefits under drought conditions. Shamuyarira et al. (2022) pinpointed that wheat genotypes with higher root biomass were relatively drought tolerant and may have a greater capacity to contribute to carbon (C) sequestration in agricultural soils. This agrees with Fan et al. (2019), who reported 81% increase in C inputs in Canada between 1971 and 2015 through growing crops that allocate more biomass below ground. The soil C inputs in wheat and maize cropping systems can increase by up to 48 g m<sup>-2</sup> and 30 g m<sup>-2</sup> respectively, from rhizodeposition after one growing season (Gregory and Atwell. 1991; Balesdent and Balabane, 1992; Hirte et al., 2018). Carbon inputs from the decomposition of root residues can also be beneficial for nutrient recycling, soil organic matter build up and maintaining soil physical and chemical properties (Amos and Walters. 2006; Bakhshandeh et al., 2019). In addition, more C sequestration into soils means less C in the atmosphere; thus, generating cultivars that transfer more carbon into soils can mitigate climate change.

Developing a new wheat ideotype with high biomass production and achieving genetic improvement for drought tolerance requires genetic variation and exploration of genetic variance components and heritability for biomass allocation traits and grain yield in new breeding populations (Dhanda et al., 2004; Khush 2013). Genetic variation and heritability estimates differ widely depending on the crop, the trait of interest, the environment and test populations and their interactions (Teklu et al., 2021). For instance, in rice Toorchi et al. (2002) reported genotypic coefficient of variation (GCV) varying from 13.46% to 20.86%, while the phenotypic coefficient of variation (PCV) ranged from 17.02% to 26.60% for root and shoot traits. In contrast, Mathew et al., (2018) recorded high GCV and PCV values for wheat root biomass and yield-related traits ranging from 43.10% to 83.80% under different moisture conditions. Several studies have reported high heritability (>60.00%) for biomass allocation traits and grain yield for wheat (Toorchi et al.,

2002; Dhanda et al., 2004; Mathew et al., 2018; Kaur et al., 2021). Conversely, other studies reported low to moderate (<60.00%) heritability (Collaku and Harrison 2005; Mohammadi 2016; Lozada and Carter 2019). The magnitude of variance components estimated in the evaluated breeding populations will be important in understanding the level of trait expression and mode of gene action controlling biomass allocation and in guiding optimal selection (Katrul et al., 2022). This information will determine the breeding strategy to adopt for efficient selection of promising drought-tolerant families for advanced testing and cultivar recommendation (Agaba et al., 2021).

High throughput screening methods are required to select drought tolerant genotypes with high yields and biomass production (Bahrami et al., 2014). Different stress levels confound the level of drought tolerance and susceptibility of genotypes. However, farmers prefer cultivars that perform well under optimum growing conditions with minimal yield losses in drought years (Dodig et al., 2012; Saeidnia et al., 2017). To select and recommend high performing genotypes, there is a need for a reliable selection index to use during drought screening (Bahrami et al., 2014). To screen and identify drought tolerant genotypes, several drought tolerance indices have been used including tolerance index (TOL) and mean productivity (MP) (Rosielle and Hamblin 1981), stress susceptibility index (SSI) (Fischer and Maurer 1978), yield stability index (YSI) (Bousslama and Schapaugh 1984), geometric mean productivity (GMP) and stress tolerance index (STI) (Fernandez 1992), yield index (YI) (Gavuzzi et al., 1997) and harmonic mean (HM) (Farshadfar et al., 2013). However, most studies evaluating drought tolerance indices have not considered the relationship of root biomass to drought tolerance in targeted selection for drought-prone areas. As a first step to developing climate-smart cultivars with drought tolerance and enhanced biomass allocation, direct and reciprocal crosses were developed from 10 pre-selected highly contrasting lines using a full diallel mating design. Consequently, the new breeding populations should be evaluated for genetic variability of drought tolerance and biomass allocation to the root system to select promising families for advanced testing and deployment. Although genetic variability studies have been done in various crops (Toorchi et al. 2002; Mengistu et al., 2020; Kaur et al., 2021), no studies have evaluated genetic variability of F<sub>2</sub> families for biomass allocation under contrasting moisture regimes in wheat. Therefore, the objective of this study was to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement.

## **5.2 Materials and methods**

### **5.2.1 Plant materials, crosses, study sites and phenotyping**

The study involved 100 bread wheat genotypes comprising 10 parental lines, 45 direct crosses and 45 reciprocal crosses developed from a full diallel mating design. The details of the plant material are presented in Chapter 3, Section 3.2.1.

The experiments were conducted in the field and in greenhouse conditions under two water regimes (drought-stressed and non-stressed conditions). The study sites, experimental layout and details on the conduct of the experiments are described in full in Chapter 3, Section 3.2.2.

### **5.2.2 Data collection**

Data were collected for six agronomic traits separately for the two water regimes at the two different sites. Detailed description of the data collected are described in Chapter 3, Section 3.2.3 for plant height (PH), kernels per spike (KPS), shoot biomass (SB), root biomass (RB), total plant biomass (PB) and grain yield (GY).

### **5.2.3 Data analyses**

#### **5.2.3.1 Analysis of variance**

The data collected were tested for normality using the Bartlett's homogeneity of variance test (Bartlett 1937). The two-site data set were subjected to a combined analysis of variance using a lattice procedure involving a three-way interaction of genotype, water regime and site, using Genstat 18th Edition (Payne, 2017). Fisher's least significance difference (LSD) procedure was used to compare mean values of test genotypes for the measured traits at the 5% significance level.

#### **5.2.3.2 Variance components estimates**

The variance components were estimated based on the estimated mean squares from the combined analysis of variance of individual water regimes according to Mather and Jinks (1971), as shown in Table 5.1.

Table 5.1. Partial analysis of variance and expected mean squares of 10 parental lines and 90 F<sub>2</sub> progenies of bread wheat evaluated across two sites

Source of variation	Df	Mean square	Expected mean square
<b>Genotype (g)</b>	$g - 1$	$MS_g$	$\sigma_e^2 + r\sigma_{gs}^2 + r\sigma_g^2$
<b>Site (s)</b>	$s - 1$	$MS_s$	-
<b>g × s</b>	$(g - 1)(s - 1)$	$MS_{gs}$	$r\sigma_{gs}^2 + \sigma_e^2$
<b>Error</b>	$s(g - 1)(r - 1)$	$Mse$	$\sigma_e^2$

$MS_g$  = mean square value for genotypes,  $MS_s$  = mean square value for sites,  $MS_{gs}$  = mean square value for genotype by site interaction,  $Mse$  = mean square value for error,  $\sigma_e^2$  = environmental variance,  $\sigma_{gs}^2$  = genotype by site variance,  $\sigma_g^2$  = genotypic variance,  $g$  = number of genotypes,  $s$  = number of sites,  $r$  = number of replications

The genotypic and phenotypic variances were calculated as shown below after partitioning of variance components:

$$\text{Genotypic variance } (\sigma_g^2) = (MS_g - r\sigma_{gs}^2)/rs$$

$$\text{Phenotypic variance } (\sigma_p^2) = (\sigma_g^2 + \sigma_{gs}^2)/(s + \sigma_e^2/rs)$$

where  $g$  = genotypes,  $s$  = sites,  $r$  = replications,  $MS_g$  = mean square for genotypes,  $MS_s$  = mean square for sites,  $MS_{gs}$  = mean square for genotype × site interaction,  $Mse$  = mean square for error,  $\sigma_g^2$  = genotypic variance,  $\sigma_{gs}^2$  = genotype by site interaction variance, and  $\sigma_e^2$  = environmental variance.

The degree of phenotypic and genotypic variability in the breeding population was estimated according to Johnson et al., (1955) as follows:

$$\text{Genotypic coefficient of variation (GCV)} = [(\sigma_g) / \bar{x}] \times 100$$

$$\text{Phenotypic coefficient of variation (PCV)} = [(\sigma_p) / \bar{x}] \times 100$$

where,  $\sigma_g$  = genotypic standard deviation,  $\sigma_p$  = phenotypic standard deviation, and  $\bar{x}$  = mean of all genotypes for a specific trait

The broad sense heritability ( $H^2$ ) was calculated as the ratio of genotypic variance and the phenotypic variance and expressed as a percentage below:

$$H^2 = [\sigma_g^2 / \sigma_p^2] \times 100$$

where  $\sigma_g$  = genotypic variance,  $\sigma_p$  = phenotypic variance

The expected genetic advance (GA) and genetic advance as a percentage of the mean (GAM) were calculated according to Allard (1960) based on the following formulae:

$$GA = k \times H^2 \times \sigma_p$$

$$GAM = [GA/\bar{x}] / 100$$

where  $k$  = coefficient of selection intensity (assuming 10% selection intensity),  $H^2$  = broad sense heritability,  $\sigma_p$  = phenotypic standard deviation, and  $\bar{x}$  = mean of all genotypes for a specific trait

### 5.2.3.3 Drought tolerance indices

In this study, nine different drought tolerant indices were calculated, including tolerance index (TOL), mean productivity (MP), stress susceptibility index (SSI), yield stability index (YSI), geometric mean productivity (GMP), stress tolerance index (STI), yield index (YI), harmonic mean (HM) and drought sensitivity index (DSI) based on grain yield under drought-stressed and non-stressed conditions. Calculations of drought tolerance indices were based on the following equations and references.

1. TOL =  $Y_p - Y_s$  (Rosielle and Hamblin, 1981)
2. MP =  $\frac{Y_p + Y_s}{2}$  (Rosielle and Hamblin, 1981)
3. SSI =  $\frac{1 - \frac{Y_s}{Y_p}}{1 - \frac{\bar{Y}_s}{\bar{Y}_p}}$  (Fischer and Maurer, 1978)
4. YSI =  $\frac{Y_s}{Y_p}$  (Bousslama and Schapaugh, 1984)
5. GMP =  $(Y_p \times Y_s)^{0.5}$  (Fernandez, 1992)
6. STI =  $\frac{Y_p \times Y_s}{(\bar{Y}_p)^2}$  (Fernandez, 1992)
7. YI =  $\frac{Y_s}{\bar{Y}_p}$  (Gavuzzi et al., 1997)
8. HM =  $\frac{2Y_s Y_p}{Y_s + Y_p}$  (Farshadfar et al., 2013)
9. DSI =  $\frac{Y_p + Y_s}{Y_p}$  (Farshadfar and Javadinia, 2011)

where  $Y_p$  = grain yield of an individual genotype under non-stressed conditions,  $Y_s$  = grain yield for an individual genotype under drought stressed conditions,  $\bar{Y}_p$  is the mean yield of all

genotypes under non-stressed conditions,  $\bar{Y}_s$  is the mean yield of all genotypes under drought stressed conditions, TOL = tolerance index, MP = mean productivity, SSI = stress susceptibility index, YSI = yield stability index, GMP = geometric mean productivity, STI = stress tolerance index, YI = yield index, HM = harmonic mean and DSI = drought sensitivity index.

#### **5.2.3.4 Correlation and principal component analysis**

Pearson correlation coefficients were calculated based on mean values across sites to determine the bivariate associations for  $Y_p$ ,  $Y_s$ , root biomass under non-stressed ( $RB_p$ ) and drought-stressed ( $RB_s$ ) conditions and drought tolerance indices. Correlations were computed using IBM SPSS Statistics for Windows, Version 24.0. Principal component analysis (PCA) and biplot analysis were computed to determine the association of  $Y_p$ ,  $Y_s$ ,  $RB_p$ ,  $RB_s$  and drought tolerance indices and identify the most efficient drought tolerance indices to guide the selection of relatively drought-tolerant families for genetic advancement. The PCA was calculated in R statistical software (R Core Team, 2019).

### **5.3 Results**

#### **5.3.1 Analysis of variance**

The ANOVA for the biomass allocation traits and grain yield showed significant differences for PH, KPS, SB, RB, PB and GY (Table 5.2). The family  $\times$  water regime interaction was significant only for GY. On the other hand, all the measured traits had a significant family-by-site interaction effects.

Table 5.2. Mean squares and significant tests from the combined analysis of variance for yield components and biomass traits of 10 bread wheat parental lines, 45 direct crosses and 45 reciprocal crosses evaluated at two sites under drought-stressed and non-stressed conditions

SOV	d.f	PH	KPS	SB	RB	PB	GY
<b>Replication</b>	1	142.45	212.15	4484	10390.90***	220237.00*	43869.00*
<b>Block</b>	18	176.89*	115.63*	25982.00***	994.50*	67304	21502.00**
<b>Family</b>	99	243.27***	142.25***	18128.00***	769.50**	69654.00***	14638.00**
<b>Water Regime (WR)</b>	1	11091.44***	7189.67***	938657.00***	10709.50***	12251041.00***	5465271.00***
<b>Site</b>	1	89648.69***	67179.66***	2054036.00***	24588.50***	1132252.00***	165356.00***
<b>Family.WR</b>	99	104.61	71.7	11642	631.9	53980	13481.00*
<b>Family.Site</b>	98	149.27***	94.62*	17491.00***	756.10*	67155.00**	14496.00*
<b>Family.WR.Site</b>	97	116.64	72.21	12166	577.7	45619	12154
<b>Residual</b>	368	91.79	66.81	10071	533	43026	10167

SOV = source of variation, d f = degrees of freedom, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ )

### 5.3.2 Mean performance of parents and F<sub>2</sub> families

The mean performance of the parental lines, direct crosses and reciprocal crosses are shown in Appendix 5.1. The mean PH under non-stressed conditions was 87.27 cm compared to 79.76 cm under drought-stressed conditions. The means for KPS were at 38.69 under non-stress and reduced to 32.45 under drought. There were 27.17% and 40.21% reductions in mean SB and PB respectively due to the drought effect. Conversely, RB increased by 22.51% under drought-compared to that under non-stressed conditions. Grain yield was severely affected by drought resulting in a 54.47% drop in grain yield between drought- and non-stressed conditions. The parental line LM75 (267.32 gm<sup>-2</sup>) and the reciprocal cross LM26 x BW140 (241.33 gm<sup>-2</sup>) had the highest GY under drought, while the reciprocal cross LM71 x LM26 (497.95 gm<sup>-2</sup>) and the direct cross LM26 x LM75 (481.21 gm<sup>-2</sup>) had the highest grain yield under non-stressed conditions.

### 5.3.3 Genetic and phenotypic variance and heritability estimates

The estimates of variance components and heritability for biomass allocation traits and grain yield are presented in Table 5.3. The GCV ranged from 14.67% to 42.26% under drought and from 12.25% to 44.53% under non-stressed conditions. On the other hand, the PCV values ranged from 20.68% to 77.70% under drought conditions, whilst it ranged from 18.27% to 62.30% under non-stressed conditions. High PCV values of >50 % were observed for RB, SB, PB and GY. The GCV values were lower than PCV values for all evaluated traits under both water regimes. GCV and PCV values were higher for SB, RB, PB and GY but lower for PH and KPS.

Estimates for H<sup>2</sup> under the different water regimes were moderate (40.00% < H<sup>2</sup> < 60.00%) under drought-stressed conditions for PH (50.33%) and RB (41.61%). Also, PH (44.96%), KPS (45.14%), SB (46.51%) and PB (44.17%) showed moderate heritability under non-stressed conditions. Grain yield (18.79%) had the lowest heritability under drought-stressed conditions, whilst RB (24.75%) had the lowest under non-stressed conditions. The GAM varied from 0.26% to 3.76% and from 0.21% to 3.58% under drought- and non-stressed conditions, respectively. The presence of moderate heritability and GAM were observed for RB under drought and for KPS under non-stressed conditions. In comparison, all other traits had relatively low heritability and GAM values.

Table 5.3. Estimates of variance components for biomass allocation and grain yield traits of 10 bread wheat parental lines and 90 F<sub>2</sub> progenies evaluated across two sites under drought-stressed and non-stressed conditions

<b>Variance components: drought-stress</b>								
<b>Traits</b>	$\sigma^2_g$	$\sigma^2_p$	<b>H<sup>2</sup> (%)</b>	<b>Mean</b>	<b>GCV (%)</b>	<b>PCV (%)</b>	<b>GA</b>	<b>GAM (%)</b>
<b>PH</b>	136.92	272.02	50.33	79.76	14.67	20.68	1.46	1.83
<b>KPS</b>	50.54	144.24	35.04	32.45	21.91	37.01	1.22	3.76
<b>RB</b>	244.10	586.70	41.61	38.06	41.05	63.64	1.33	3.49
<b>SB</b>	6217.00	21019.00	29.58	186.60	42.26	77.70	1.12	0.60
<b>PB</b>	12695.50	55609.00	22.83	384.80	29.28	61.28	0.98	0.26
<b>GY</b>	1561.00	8308.00	18.79	141.20	27.98	64.55	0.89	0.63
<b>Variance components: non-stress</b>								
<b>Traits</b>	$\sigma^2_g$	$\sigma^2_p$	<b>H<sup>2</sup> (%)</b>	<b>Mean</b>	<b>GCV (%)</b>	<b>PCV (%)</b>	<b>GA</b>	<b>GAM (%)</b>
<b>PH</b>	114.26	254.12	44.96	87.27	12.25	18.27	1.38	1.58
<b>KPS</b>	92.11	204.07	45.14	38.69	24.81	36.92	1.38	3.58
<b>RB</b>	136.15	550.00	24.75	30.99	37.65	75.68	1.02	3.31
<b>SB</b>	13018.00	27988.00	46.51	256.20	44.53	65.30	1.40	0.55
<b>PB</b>	64291.50	145542.00	44.17	643.60	39.40	59.28	1.37	0.21
<b>GY</b>	13708.00	37327.00	36.72	310.10	37.76	62.30	1.25	0.40

PH = plant height, KPS = kernels per spike, RB = root biomass, SB = shoot biomass, PB = total plant biomass, GY = grain yield,  $\sigma^2_g$  = genotypic variance,  $\sigma^2_p$  = phenotypic variance, H<sup>2</sup> = broad sense heritability, GCV = genetic coefficient of variation, PCV = phenotypic coefficient of variation, GA = genetic advance, GAM = genetic advance as a percentage of mean

### 5.3.4 Performance of genotypes based on drought tolerance indices

Nine drought tolerance indices were calculated for each genotype based on grain yield under drought-stressed ( $Y_s$ ) and non-stressed ( $Y_p$ ) conditions to identify the best families for genetic advancement (Appendix 5.2). Root biomass under drought-stressed ( $RB_s$ ) and non-stressed ( $RB_p$ ) conditions were also recorded. The families LM47  $\times$  BW152, BW140  $\times$  LM71 and BW140  $\times$  LM48 scored low values for SSI, TOL and DSI and high values for YSI and YI, suggesting their drought tolerance. High values for GMP, STI, HM and MP were recorded for BW162  $\times$  LM75 and LM48  $\times$  BW140 and the parental line LM75.

Pearson correlation coefficients between  $Y_s$ ,  $Y_p$ ,  $RB_s$ ,  $RB_p$  and drought tolerance indices are presented in Table 5.4. Grain yield under drought stress ( $Y_s$ ) and non-stressed ( $Y_p$ ) conditions had a weak and non-significant correlation ( $r = -0.02$ ). There was a strong correlation of  $Y_s$  with YI ( $r = 1.00$ ) and HM ( $r = 0.88$ ), whilst  $Y_p$  had strong positive correlations with TOL (0.92) and MP (0.92). Notably, STI and GMP had strong positive correlations ( $r > 0.65$ ) with both  $Y_s$  and  $Y_p$ . None of the drought tolerance indices had strong positive correlation with either  $RB_s$  or  $RB_p$  except TOL that had moderate correlations ( $0.40 < r < 0.60$ ) with  $RB_p$ . Some of the drought tolerance indices had a perfect correlation ( $r = 1.00$ ) with each other such as STI and GMP, as well as SSI and DSI.

Principal component analysis was performed using  $Y_s$ ,  $Y_p$ ,  $RB_s$ ,  $RB_p$  and drought tolerance indices to determine the most influential components and elucidate the relationship between drought tolerance indices and the evaluated genotypes (Table 5.5, Figure 5.1). The first two principal components (PCs) explained a total of 85.87% of the drought tolerance variation among the genotypes, with PC1 explaining 44.45% and PC2 41.42% of the total variation (Table 5.5). There was a positive correlation between PC1 with  $Y_p$ , SSI, TOL, MP, YSI and DSI, while PC2 was correlated with  $Y_s$ , GMP, STI, YI and HM. The reciprocal crosses scored relatively higher for PC1 (genotype 61 = LM48  $\times$  BW140, genotype 78 = LM71  $\times$  LM26) and PC2 (genotype 68 = LM70  $\times$  BW141, genotype 69 = LM70  $\times$  BW152) (Figure 5.1, Appendix 5.2). Direct crosses had some genotypes that scored high for PC1 (genotype 35 = LM26  $\times$  LM75, genotype 45 = LM71  $\times$  LM75) but most appeared poor for PC2. The parental genotypes scored poor for PC1 and PC2, except for genotype 100 (LM75), which scored very high for PC2. Stress tolerance index and GMP had strong relationships with both  $Y_s$  and  $Y_p$ .

Table 5.4. Correlation coefficients and significance tests for grain yield, root biomass and drought tolerance indices of 10 bread wheat parental lines and 90 F<sub>2</sub> progenies evaluated at two sites

Traits	Ys	Yp	RBs	RBp	GMP	STI	SSI	TOL	MP	YSI	YI	HM	DSI
Ys	1												
Yp	-0.02	1											
RBs	0.25*	0.09	1										
RBp	-0.03	0.43**	0.08	1									
GMP	0.68**	0.72**	0.22*	0.31**	1								
STI	0.68**	0.71**	0.22*	0.31**	1.00**	1							
SSI	-0.66**	0.71**	-0.11	0.36**	0.09	0.08	1						
TOL	-0.41**	0.92**	-0.02	0.40**	0.39**	0.39**	0.91**	1					
MP	0.38**	0.92**	0.18	0.39**	0.93**	0.92**	0.40**	0.69**	1				
YSI	0.66**	-0.71**	0.11	-0.36**	-0.09	-0.08	-1.00**	-0.91**	-0.40**	1			
YI	1.00**	-0.02	0.25*	-0.03	0.68**	0.68**	-0.66**	-0.41**	0.38**	0.66**	1		
HM	0.88**	0.43**	0.23*	0.19	0.94**	0.93**	-0.23*	0.05	0.74**	0.23*	0.88**	1	
DSI	-0.66**	0.71**	-0.11	0.36**	0.09	0.08	1.000**	0.91**	0.40**	-1.00**	-0.66**	-0.23*	1

Ys = yield under drought-stressed conditions, Yp = yield under non-stressed conditions, RBs = root biomass under drought-stressed conditions, RBp = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

Table 5.5. Principal component analysis of grain yield, root biomass and drought indices of 10 parental lines, 45 direct crosses and 45 reciprocal crosses of bread wheat

	Eigenvalue	Per Var (%)	Cum Var (%)	Ys	Yp	RBs	RBp	GMP	STI	SSI	TOL	MP	YSI	YI	HM	DSI
PC1	5.78	44.45	44.45	0.75	<b>16.12</b>	0.03	4.55	5.71	5.60	<b>12.62</b>	<b>16.08</b>	<b>11.34</b>	<b>12.62</b>	0.75	1.23	<b>12.62</b>
PC2	5.38	41.42	85.87	<b>17.64</b>	0.72	1.79	0.11	<b>12.29</b>	<b>12.32</b>	4.67	0.75	5.99	4.67	<b>17.64</b>	<b>16.72</b>	4.67

PC = principal component, Ys = yield under drought-stressed conditions, Yp = yield under non-stressed conditions, RBs = root biomass under drought-stressed conditions, RBp = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index, **Bold values indicate high positive loadings for either PC1 or PC2**

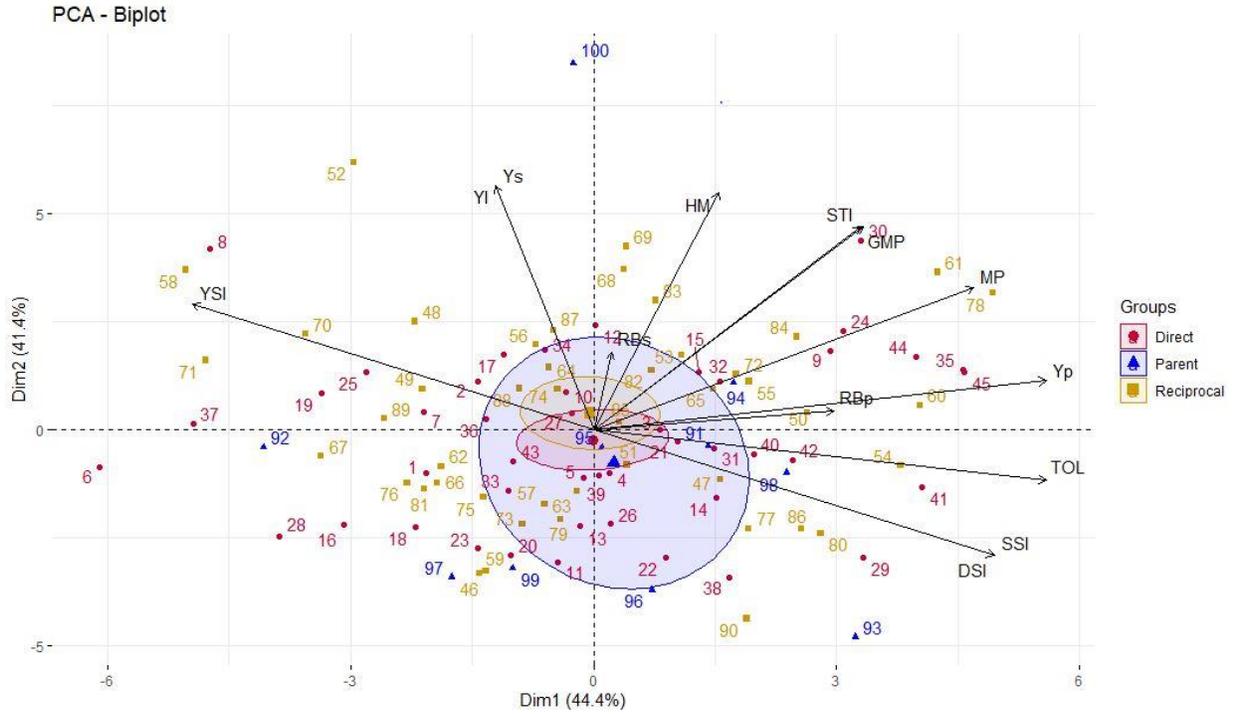


Figure 5.1. Principal component biplot showing the relationship of  $Y_s$ ,  $Y_p$ , RBs, RBp and drought tolerance indices of 10 parental lines, 45 direct crosses and 45 reciprocal crosses of bread wheat evaluated under drought stressed and non-stressed conditions at two sites.;  $Y_s$  = yield under drought-stressed conditions,  $Y_p$  = yield under non-stressed conditions, RBs = root biomass under drought-stressed conditions, RBp = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

## 5.4 Discussion

### 5.4.1 Genetic variability among parental genotypes and F<sub>2</sub> families

A highly significant difference existed among the genotypes for biomass allocation and grain yield (Table 5.2). This suggests the presence of genetic variability that is useful for trait integration to warrant the selection of drought-tolerant wheat cultivars with high biomass production agreeing with the study of Kell (2011). Moreover, there was a significant genotype x site interaction effect for GY, showing the differential responses of the genotypes in the various test locations. Therefore, it is essential to apply a less stringent selection intensity to reduce the risk of elimination of high-yielding genotypes when selecting promising progenies in this panel (Ongom et al., 2021)

There were significant differences between GCV and PCV for SB, RB, PB and GY under both water regimes, suggesting strong impact of the environment on these traits. Therefore, there is a need for genetic advancement of superior families at multiple sites to reduce the confounding effects of the environment (Zalapa et al., 2008). For PH and KPS, the deviation of the GCV from the PCV was relatively small compared to the other measured traits. This reflect a more significant influence of the genetic component on these traits with minimum environmental effects, which increases selection efficiency for these traits (Mohammadi and Pourdad 2009). Plant height controlling gene, *Rht25b*, has been reported to have positive pleiotropic effects on yield influencing traits such as heading time, spike-related characteristics and kernel weight (Mo et al., 2018). Therefore, an ideal PH can be selected, to optimise the harvest index and partitioning of spike dry matter for efficient grain production (Rivera-Amado et al., 2019).

Heritability estimates are essential in determining the effectiveness of selecting superior genotypes and families. Traits with high heritability values may be selected in the early generations to reduce the cost associated with the advancement of large numbers of genotypes (Agaba et al., 2021). The moderate  $H^2$  estimates recorded for PH and RB under drought and PH, KPS, SB and PB under non-stressed conditions suggest that the impact of the genes and the environment are expressed in the phenotype. Therefore, selection for these traits can be made with average levels of efficiency (Mengistu et al., 2020). On the other hand,  $H^2$  estimates were low for GY under drought-stressed conditions suggesting that a large proportion of the phenotypic variability of grain yield under sub-optimal environments is due to the environment (Mohammadi and Pourdad 2009). This was expected given that GY is a product of different yield components and agronomic traits affected

by drought (Shukla et al., 2015). Low heritability estimates for grain yield compared to other agronomic traits are expected and reported in other studies (Mohammadi and Pourdard 2009; Mohammadi 2016; Katral et al., 2022). Root biomass had higher  $H^2$  under drought than under non-stressed conditions, suggesting that genomic regions responsible for RB are activated or up-regulated under moisture stress conditions (Comas et al., 2013; Rasool et al., 2022). In addition, RB had the highest GAM under drought, indicating that selection for increased RB development will be more effective under drought-stressed conditions. Similarly, KPS had the highest GAM under non-stressed conditions and selection for KPS under this condition will result in the greatest genetic gain compared to other measured traits (Shamuyarira et al., 2022).

#### **5.4.2 Drought tolerance evaluation**

In the literature, there are several drought tolerance indices (Fischer and Maurer 1978; Rosielle and Hamblin 1981; Bouslama and Schapaugh 1984; Fernandez 1992; Gavuzzi et al., 1997; Farshadfar et al., 2013; Farshadfar and Javadinia 2011). These indices have been used to identify and select drought-tolerant genotypes for either cultivar release or genetic advancement. However, the effectiveness of drought tolerance indices may be affected by the test genotypes, stress severity, growing environment, and management practices and their interaction (Cabello et al., 2013). The families LM47 × BW152, BW140 × LM71 and BW140 × LM48 that were identified as drought tolerant by SSI, TOL, DSI, YSI and YI were characterised by minor yield differences under drought-stressed and non-stressed conditions. These indices identified genotypes that performed well under drought stress with little consideration of the upper bound of yield under non-stressed conditions. Notably, high correlations were observed between these indices, especially SSI and DSI, suggesting that these indices can be used interchangeably to identify genotypes that have high yield potential under drought but low yield under optimum growing conditions (Bahrami et al., 2014; Sánchez-Reinoso et al., 2020). These indices are ideal for selecting genotypes for environments with erratic and low rainfall and therefore need stable genotypes with minimum yield fluctuations (Mohammadi 2016).

High values for STI, GMP, HM and MP were noted for BW162 × LM75 and LM48 × BW140 and LM75 (Appendix 5.3), indicating that these indices identified similar genotypes as drought tolerant. However, the genotype ranking slightly differed among these indices. Based on the correlation values, STI and GMP had strong positive associations with both  $Y_p$  and  $Y_s$ , while HM

had a stronger relationship with  $Y_s$  and MP with  $Y_p$ . These relationships suggest that MP would be biased towards genotypes with high yield under non-stressed conditions, while HM would favour those with higher yield under stress (El-Hendawy et al., 2017). The low correlations observed for the indices with root biomass suggest that drought tolerance is a polygenic trait that does not depend on root development alone, but other drought-related traits such as stomatal conductance, stay greenness, osmotic adjustment, canopy senescence and water use efficiency (Deikman et al., 2012; Kipp et al., 2013; Lobos et al., 2014).

To be adopted by farmers, drought-tolerant genotypes must have high yield potential at least comparable to the currently grown cultivars under optimum growing conditions but suffer less yield loss under stress than the local checks (Deikman et al., 2012; Saeidnia et al., 2017). Therefore, it is important to use an index to identify genotypes that perform well under drought and non-stressed conditions. The PCA done using drought tolerance indices showed that PC1 was more correlated to yield potential under non-stressed conditions, whereas PC2 was related to yield under drought stress. Consequently, genotypes that scored high for both PC1 and PC2, such as BW162 × LM75 and LM48 × BW140 were considered stable and high yielding across drought-stressed and non-stressed conditions (Bahrami et al., 2014). The PCA biplot showed that more reciprocal crosses scored high for PC1 and PC2 than direct crosses indicating that reciprocal genetic effects may contribute to increased drought tolerance and stability in wheat. The parental line LM75 scored very high for PC2 and surpassed all the other test genotypes for yield under drought and should be further evaluated in multi-environment trials against local checks for possible release.

Based on the correlations and PCA biplot analysis, GMP and STI had the strongest correlations with both  $Y_p$  and  $Y_s$  and would be the best indices to use to select families that are drought-tolerant and maintain high yields in both drought-stressed and non-stressed conditions (Ebrahimiyan et al., 2012; Bahrami et al., 2014). The utility of GMP to discriminate drought-tolerant genotypes that score highly under drought and non-stressed conditions have been reported for different crops, including wheat (El-Hendawy et al., 2017), maize (Jafari et al., 2009), common bean (Schneider et al., 1997) and smooth brome grass (Saeidnia et al., 2017).

## 5.5 Conclusions

The direct crosses BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75, and the reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 were identified as drought tolerant and are recommended for genetic advancement (Appendix 5.3). The high root biomass production these families' will contribute to carbon inputs through rhizodeposition and accumulation of root dry matter in agricultural soils. Further research should also consider nutrient uptake and transfer of atmospheric carbon to soils for maintaining high GY, soil quality and mitigating climate change.

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Appendix 5.1. Mean values for biomass allocation traits and grain yield of 10 bread wheat parental lines and 90 F<sub>2</sub> families based on grain yield under drought-stressed conditions evaluated at two sites under two water regimes

Genotype	PH		KPS		SB		RB		PB		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
LM75	92.58	89.03	35.54	39.96	239.58	297.30	49.96	70.25	682.40	680.32	335.78	267.32
LM26 x BW140	80.88	75.20	37.33	36.00	233.25	199.69	27.20	54.92	572.95	536.96	267.10	241.33
BW140 x LM71	78.75	76.48	41.38	39.75	170.75	177.42	13.00	32.88	443.28	458.36	221.82	215.63
LM47 x BW152	83.30	92.13	35.79	40.88	191.85	301.13	13.29	53.94	417.31	594.91	209.51	204.99
LM70 x BW152	95.45	85.00	42.63	32.25	308.13	201.93	15.19	40.57	733.45	479.53	350.53	202.60
LM70 x BW141	90.45	83.73	45.21	40.21	158.63	188.03	27.72	30.77	584.77	448.72	340.52	196.52
BW162 x LM75	94.85	92.03	39.67	38.25	289.19	252.30	37.16	64.09	764.35	537.48	436.16	188.96
LM75 x BW141	86.23	79.55	41.96	34.29	231.36	212.91	33.32	28.82	669.32	457.69	345.85	184.58
BW152 x BW141	86.55	84.90	41.83	32.83	147.57	265.18	28.12	65.07	514.11	542.62	255.81	181.52
LM70 x BW162	84.58	78.58	36.33	33.88	214.65	173.67	26.08	53.36	468.07	438.48	223.02	180.73
BW141 x LM26	89.43	75.93	36.54	37.71	338.36	174.62	42.10	28.91	657.34	289.35	313.93	178.91
LM48 x BW140	85.58	72.13	48.42	33.88	369.12	155.91	48.37	32.60	962.54	396.74	465.86	177.98
LM75 x LM47	95.75	91.15	37.25	36.00	228.06	288.63	28.09	37.59	612.34	519.75	304.43	177.73
LM70 x LM26	85.60	83.67	34.96	40.17	197.57	242.52	15.81	54.35	441.47	515.55	194.95	172.00
LM47 x BW140	86.55	79.30	34.08	34.67	211.62	216.17	24.29	54.99	582.29	486.55	296.05	171.01
LM26 x LM71	93.13	87.20	36.75	34.83	306.70	231.70	41.22	45.08	640.76	476.35	290.47	170.58
BW141 x LM75	95.43	87.18	43.54	31.79	304.99	207.99	19.75	49.06	607.51	455.56	285.74	169.67
BW162 x LM26	83.45	84.83	42.38	34.25	240.26	243.97	38.05	54.59	544.58	427.52	227.57	166.10
LM26 x BW141	90.40	71.65	41.75	38.79	217.49	147.15	37.95	21.70	662.21	362.72	347.67	165.70
LM71 x LM26	88.70	78.38	35.21	31.21	388.93	199.61	41.80	50.42	1013.32	443.01	497.95	164.94
BW152 x LM75	89.28	83.60	40.67	35.46	302.57	211.06	44.54	32.87	836.91	435.93	418.63	164.10
LM48 x BW162	98.80	84.33	38.67	36.50	284.74	154.69	11.01	44.14	590.89	404.77	305.60	164.01
LM75 x BW152	93.33	82.68	41.92	37.75	264.24	200.45	31.95	41.28	768.67	396.66	403.83	163.14
BW152 x LM26	81.58	75.48	30.33	30.17	194.58	126.02	23.09	30.36	473.93	346.79	219.02	162.75
BW140 x LM75	85.55	71.70	31.63	28.96	327.32	174.01	68.54	30.95	851.62	391.42	394.29	159.36
BW140 x BW152	85.00	80.60	36.42	28.29	298.51	203.99	28.78	63.06	501.67	402.42	265.31	159.29
BW162 x BW140	75.90	73.18	33.92	30.17	168.03	170.87	16.06	57.73	479.04	417.75	252.10	158.99
LM75 x BW140	86.10	78.30	38.92	25.92	262.87	186.13	30.43	47.17	685.52	419.07	335.23	158.77
LM71 x BW140	75.78	75.58	38.08	34.46	329.99	204.43	31.23	28.99	699.22	418.77	295.56	158.42
BW141 x LM70	96.38	91.18	38.83	34.63	375.67	359.04	22.18	25.14	822.03	569.22	362.55	158.15
LM75 x LM48	83.30	86.33	36.08	35.96	248.28	227.76	24.20	52.55	541.43	464.02	282.93	157.01
BW141 x BW152	99.40	82.03	38.63	33.43	354.91	175.07	38.04	34.05	737.05	392.32	294.10	156.58
LM75 x LM70	91.50	88.45	38.46	34.79	228.70	172.53	28.18	17.56	528.53	371.14	232.17	154.74
LM70 x LM47	96.28	92.75	43.67	34.25	275.18	286.85	28.72	36.80	842.77	484.41	374.15	154.45
LM26 x LM48	85.08	79.63	44.08	45.58	234.84	133.14	29.92	32.37	692.11	345.19	365.26	153.57
BW162	93.13	70.05	38.88	23.67	307.79	124.96	26.75	28.12	771.99	331.71	373.88	152.67
BW140 x LM70	79.50	80.60	39.46	33.92	228.48	143.97	28.62	47.66	540.94	369.63	242.60	152.14
LM70 x LM75	97.43	94.90	38.08	41.33	371.09	265.52	47.30	29.55	947.47	472.59	452.21	151.73
LM47 x LM70	85.93	85.78	28.33	31.08	181.44	246.43	24.38	38.46	412.26	461.89	176.44	151.28
LM47 x LM48	89.30	88.68	43.17	35.25	248.33	251.02	25.92	27.09	586.48	480.80	266.87	151.00
LM26 x BW162	88.08	78.15	43.75	34.17	264.61	272.42	34.58	50.50	737.26	498.24	374.41	149.85
LM48 x LM26	82.05	76.75	51.25	37.96	223.14	231.05	26.10	49.37	673.73	454.77	362.82	149.02

NS = non-stressed conditions, DS = drought-stressed conditions, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>) and GY = grain yield (g m<sup>-2</sup>)

Appendix 5.1 continued

Genotype	PH		KPS		SB		RB		PB		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
<b>BW162 x LM48</b>	85.03	80.43	47.75	35.54	270.60	218.48	34.92	56.46	647.42	446.25	292.22	146.42
<b>BW141</b>	74.60	74.95	35.63	34.04	167.72	164.62	15.23	23.32	411.06	358.36	194.97	145.66
<b>LM75 x BW162</b>	89.40	81.23	34.38	30.75	300.98	176.51	33.09	30.00	701.57	375.95	314.11	144.82
<b>BW140 x BW162</b>	84.70	74.30	32.89	36.08	244.74	115.98	38.52	16.51	667.47	299.28	328.38	142.56
<b>LM71 x LM75</b>	86.15	82.08	39.29	30.79	413.78	184.35	43.39	38.42	1019.04	389.43	480.24	142.45
<b>LM70 x BW140</b>	86.00	81.80	33.42	26.46	156.74	149.50	45.10	17.02	435.10	332.62	197.30	141.96
<b>LM26 x LM75</b>	91.40	86.95	37.42	33.54	350.90	211.09	40.12	53.31	954.03	429.96	481.21	141.50
<b>BW162 x BW141</b>	95.23	84.93	38.88	32.71	266.05	180.52	75.71	43.27	776.54	386.17	371.60	138.78
<b>BW140 x LM48</b>	76.40	73.25	28.75	34.04	112.54	125.04	7.14	23.04	278.22	308.84	151.68	137.40
<b>LM26</b>	83.90	69.05	44.58	41.63	291.13	122.65	17.21	28.51	674.12	276.83	312.63	137.19
<b>LM48 x BW141</b>	88.63	70.08	36.38	34.46	287.87	156.44	39.73	24.30	602.09	340.23	234.61	136.32
<b>LM47 x LM26</b>	90.48	86.30	41.11	34.63	282.00	192.87	51.35	28.92	804.19	380.20	449.20	135.81
<b>BW140 x BW141</b>	74.90	61.03	30.71	29.75	167.00	121.89	20.39	20.09	460.77	300.00	238.01	135.06
<b>BW152 x LM48</b>	91.00	81.90	50.33	38.63	267.76	178.29	22.87	38.54	692.08	374.66	343.12	134.90
<b>BW140</b>	79.20	78.55	48.92	38.13	281.02	169.50	27.62	42.47	656.31	365.69	353.33	131.38
<b>LM70 x LM71</b>	81.88	89.70	45.06	35.08	186.01	289.16	22.67	64.86	522.58	507.64	266.99	131.30
<b>LM26 x LM47</b>	93.15	85.23	42.63	31.46	322.08	166.32	37.34	36.65	768.22	356.54	349.40	131.25
<b>BW162 x BW152</b>	90.60	80.48	37.92	31.04	242.65	244.84	53.62	32.65	644.57	455.70	297.69	130.49
<b>LM71 x BW152</b>	76.78	76.75	29.75	28.92	225.04	163.97	21.24	34.45	604.82	359.81	227.61	130.41
<b>LM48 x LM47</b>	96.33	75.65	36.83	28.38	299.65	120.72	26.80	30.80	552.61	303.67	235.58	130.04
<b>BW140 x LM26</b>	85.83	78.45	35.54	28.88	283.59	150.38	31.09	24.11	670.11	325.65	303.78	129.20
<b>LM47 x LM75</b>	87.90	82.05	33.56	26.08	254.44	212.38	33.94	31.35	634.92	393.28	296.19	127.82
<b>LM26 x LM70</b>	92.78	82.68	35.89	34.67	369.95	197.27	31.99	17.41	625.15	395.97	258.98	127.72
<b>LM71 x LM70</b>	74.63	78.40	28.54	25.83	138.22	146.78	18.28	41.87	411.76	337.39	233.06	127.13
<b>LM48 x LM75</b>	89.35	69.80	46.50	32.88	275.22	123.82	25.69	21.65	765.71	237.56	397.27	125.23
<b>LM48 x LM70</b>	88.75	85.33	39.50	37.21	337.22	181.24	18.41	59.07	800.17	385.80	379.95	124.35
<b>LM48 x BW152</b>	83.80	87.43	39.88	29.21	174.58	200.71	50.77	28.29	546.33	346.80	274.34	124.07
<b>BW140 x LM47</b>	91.88	79.45	32.96	26.88	184.46	230.98	46.98	69.38	556.07	444.20	277.45	122.94
<b>LM71 x BW141</b>	74.00	77.18	36.08	30.50	162.61	160.60	23.11	45.84	478.25	349.70	250.02	122.44
<b>BW141 x LM71</b>	84.18	65.05	31.04	26.83	173.86	96.06	20.55	18.39	427.39	231.54	199.13	119.20
<b>LM70</b>	91.08	84.98	44.21	36.25	365.06	245.33	19.11	42.40	847.96	426.63	396.39	118.71
<b>BW152 x BW140</b>	86.08	74.33	46.38	20.39	288.63	160.45	23.31	53.34	730.11	393.69	357.41	118.60
<b>BW152 x BW162</b>	80.85	73.40	38.17	28.13	170.07	131.74	18.00	17.57	450.42	272.57	224.23	117.65
<b>LM26 x BW152</b>	91.10	80.73	48.54	30.29	348.96	157.93	44.96	27.50	910.06	322.86	441.14	117.46
<b>BW141 x LM48</b>	84.13	72.60	41.50	32.44	229.43	119.85	23.30	18.31	683.91	280.77	356.58	117.25
<b>LM70 x LM48</b>	93.90	91.30	53.67	23.67	180.83	128.33	10.03	12.15	516.84	287.19	271.77	116.67
<b>LM47 x BW141</b>	98.75	79.88	37.00	27.75	253.48	179.62	31.28	73.29	595.31	387.78	265.43	115.28
<b>LM71 x LM47</b>	88.93	83.43	45.88	33.75	244.24	167.27	26.54	28.76	545.48	284.85	276.88	115.09
<b>BW141 x LM47</b>	98.40	71.38	33.00	28.63	236.86	104.70	32.00	25.11	598.02	262.04	281.34	113.02
<b>BW162 x LM70</b>	72.35	82.08	25.00	31.79	102.23	98.74	13.59	39.68	270.87	265.10	176.69	112.73
<b>BW162 x LM47</b>	84.50	81.45	35.42	28.17	226.81	205.60	33.90	39.29	595.36	374.49	292.67	110.77
<b>BW152 x LM71</b>	83.95	83.50	31.58	34.71	151.59	189.16	42.60	44.03	562.41	357.08	226.02	105.89
<b>LM71 x BW162</b>	88.75	78.70	35.75	29.75	374.76	162.53	31.60	30.87	830.54	296.63	362.54	104.44
<b>BW152 x LM47</b>	89.73	77.03	41.38	29.79	269.27	148.63	23.75	36.37	585.16	306.76	249.69	104.06

NS = non-stressed conditions, DS = drought-stressed conditions, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass (g m<sup>-2</sup>), RB = root biomass (g m<sup>-2</sup>), PB = total plant biomass (g m<sup>-2</sup>) and GY = grain yield (g m<sup>-2</sup>)

Appendix 5.1 continued

Genotype	PH		KPS		SB		RB		PB		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
<b>LM48 x LM71</b>	89.50	79.65	56.13	33.67	326.32	221.77	36.43	82.97	897.12	424.90	456.72	102.69
<b>LM75 x LM26</b>	89.48	74.53	42.08	29.13	274.35	102.73	26.17	30.51	764.08	252.22	396.20	101.69
<b>BW141 x BW162</b>	85.73	69.03	40.63	26.83	186.70	153.22	25.53	33.58	525.70	304.95	267.93	100.99
<b>LM71</b>	73.38	77.50	27.00	27.00	216.93	130.79	36.02	28.57	593.20	277.39	241.39	100.87
<b>LM48</b>	82.40	67.25	38.63	30.00	153.67	106.63	13.73	21.78	434.85	208.83	228.59	100.27
<b>BW141 x BW140</b>	77.60	66.63	30.63	22.46	165.03	125.72	24.59	27.37	462.64	270.09	233.34	100.01
<b>BW152 x LM70</b>	94.23	85.00	40.46	25.21	267.00	272.00	54.38	28.83	672.66	360.14	300.24	99.55
<b>LM47 x BW162</b>	87.35	83.18	37.21	28.38	204.81	176.25	41.11	36.82	510.12	329.31	225.81	99.36
<b>LM71 x LM48</b>	92.48	87.98	39.79	38.29	321.24	196.36	58.69	40.68	824.41	353.02	379.90	99.13
<b>BW162 x LM71</b>	90.45	68.78	38.25	25.42	334.12	103.75	25.92	14.65	809.10	225.54	432.71	91.57
<b>LM47 x LM71</b>	93.55	76.50	37.42	29.75	277.87	196.21	27.94	31.15	715.38	283.55	350.05	89.96
<b>LM47</b>	90.13	71.33	34.33	24.42	271.05	151.17	22.85	32.64	657.22	287.85	310.53	88.92
<b>LM75 x LM71</b>	84.53	84.05	43.92	33.06	323.36	347.87	46.38	73.42	763.69	505.65	336.71	72.11
<b>BW152</b>	88.65	60.45	31.46	26.04	399.15	121.55	31.00	23.24	922.43	199.76	420.74	67.00
<b>Mean</b>	87.27	79.76	38.69	32.45	256.20	186.60	30.99	38.06	643.60	384.80	310.10	141.20
<b>LSD</b>	13.64	13.49	12.25	11.27	141.90	142.30	31.26	33.76	342.70	250.60	183.10	95.90
<b>SEM</b>	0.64	0.71	0.58	0.48	6.97	5.52	1.24	1.51	15.71	9.04	7.87	3.37
<b>CV</b>	7.27	8.85	14.96	14.71	27.21	29.59	40.07	39.55	24.41	23.50	25.37	23.87

NS = non-stressed conditions, DS = drought-stressed conditions, PH = plant height (cm), KPS = kernels per spike, SB = shoot biomass ( $\text{g m}^{-2}$ ), RB = root biomass ( $\text{g m}^{-2}$ ), PB = total plant biomass ( $\text{g m}^{-2}$ ) and GY = grain yield ( $\text{g m}^{-2}$ ), LSD = least significance difference, SEM = standard error of mean, CV = coefficient of variation

Appendix 5.2. Yield based drought-tolerance indices for 45 direct crosses, 45 reciprocal crosses and 10 parental lines of wheat grown under drought-stressed and non-stressed conditions

Entry	Genotypes	Y <sub>s</sub>	Y <sub>p</sub>	RB <sub>s</sub>	RB <sub>p</sub>	SSI	TOL	MP	GMP	STI	YSI	YI	HM	DSI
<b>Direct crosses</b>														
1	BW140 x BW141	135 06	238 01	20 09	20 39	0 79	102 95	186 54	179 30	0 33	0 57	0 44	172 33	0 43
2	BW140 x BW152	159 29	265 31	63 06	28 78	0 73	106 02	212 30	205 57	0 44	0 60	0 51	199 06	0 40
3	BW140 x BW162	142 56	328 38	16 51	38 52	1 04	185 83	235 47	216 36	0 49	0 43	0 46	198 81	0 57
4	BW140 x LM26	129 20	303 78	24 11	31 09	1 06	174 58	216 49	198 11	0 41	0 43	0 42	181 29	0 57
5	BW140 x LM47	122 94	277 45	69 38	46 98	1 02	154 51	200 20	184 69	0 35	0 44	0 40	170 38	0 56
6	BW140 x LM48	137 40	151 68	23 04	7 14	0 17	14 28	144 54	144 37	0 22	0 91	0 44	144 19	0 09
7	BW140 x LM70	152 14	242 60	47 66	28 62	0 68	90 47	197 37	192 12	0 38	0 63	0 49	187 00	0 37
8	BW140 x LM71	215 63	221 82	32 88	13 00	0 05	6 18	218 72	218 70	0 50	0 97	0 70	218 68	0 03
9	BW140 x LM75	159 36	394 29	30 95	68 54	1 09	234 93	276 83	250 67	0 65	0 40	0 51	226 99	0 60
10	BW141 x BW152	156 58	294 10	34 05	38 04	0 86	137 52	225 34	214 60	0 48	0 53	0 50	204 36	0 47
11	BW141 x BW162	100 99	267 93	33 58	25 53	1 14	166 94	184 46	164 50	0 28	0 38	0 33	146 69	0 62
12	BW141 x LM26	178 91	313 93	28 91	42 10	0 79	135 01	246 42	236 99	0 58	0 57	0 58	227 93	0 43
13	BW141 x LM47	113 02	281 34	25 11	32 00	1 10	168 31	197 18	178 32	0 33	0 40	0 36	161 26	0 60
14	BW141 x LM48	117 25	356 58	18 31	23 30	1 23	239 33	236 92	204 47	0 43	0 33	0 38	176 47	0 67
15	BW141 x LM70	158 15	362 55	25 14	22 18	1 04	204 40	260 35	239 46	0 60	0 44	0 51	220 24	0 56
16	BW141 x LM71	119 20	199 13	18 39	20 55	0 74	79 93	159 16	154 06	0 25	0 60	0 38	149 13	0 40
17	BW141 x LM75	169 67	285 74	49 06	19 75	0 75	116 07	227 70	220 18	0 50	0 59	0 55	212 91	0 41
18	BW152 x BW162	117 65	224 23	17 57	18 00	0 87	106 58	170 94	162 42	0 27	0 52	0 38	154 33	0 48
19	BW152 x LM26	162 75	219 02	30 36	23 09	0 47	56 27	190 88	188 80	0 37	0 74	0 52	186 73	0 26
20	BW152 x LM47	104 06	249 69	36 37	23 75	1 07	145 63	176 88	161 19	0 27	0 42	0 34	146 90	0 58
21	BW152 x LM48	134 90	343 12	38 54	22 87	1 11	208 23	239 01	215 14	0 48	0 39	0 44	193 66	0 61
22	BW152 x LM70	99 55	300 24	28 83	54 38	1 23	200 68	199 90	172 89	0 31	0 33	0 32	149 53	0 67
23	BW152 x LM71	105 89	226 02	44 03	42 60	0 98	120 13	165 95	154 70	0 25	0 47	0 34	144 21	0 53
24	BW152 x LM75	164 10	418 63	32 87	44 54	1 12	254 53	291 37	262 10	0 71	0 39	0 53	235 78	0 61
25	BW162 x LM26	166 10	227 57	54 59	38 05	0 50	61 47	196 84	194 42	0 39	0 73	0 54	192 04	0 27
26	BW162 x LM47	110 77	292 67	39 29	33 90	1 14	181 90	201 72	180 05	0 34	0 38	0 36	160 71	0 62
27	BW162 x LM48	146 42	292 22	56 46	34 92	0 92	145 80	219 32	206 85	0 44	0 50	0 47	195 09	0 50
28	BW162 x LM70	112 73	176 69	39 68	13 59	0 66	63 96	144 71	141 13	0 21	0 64	0 36	137 65	0 36
29	BW162 x LM71	91 57	432 71	14 65	25 92	1 45	341 14	262 14	199 06	0 41	0 21	0 30	151 16	0 79
30	BW162 x LM75	188 96	436 16	64 09	37 16	1 04	247 20	312 56	287 08	0 86	0 43	0 61	263 69	0 57
31	LM26 x LM47	131 25	349 40	36 65	37 34	1 15	218 15	240 33	214 15	0 48	0 38	0 42	190 82	0 62
32	LM26 x LM48	153 57	365 26	32 37	29 92	1 06	211 69	259 41	236 84	0 58	0 42	0 50	216 23	0 58
33	LM26 x LM70	127 72	258 98	17 41	31 99	0 93	131 26	193 35	181 87	0 34	0 49	0 41	171 07	0 51
34	LM26 x LM71	170 58	290 47	45 08	41 22	0 76	119 89	230 52	222 59	0 52	0 59	0 55	214 94	0 41
35	LM26 x LM75	141 50	481 21	53 31	40 12	1 30	339 71	311 36	260 94	0 71	0 29	0 46	218 70	0 71
36	LM47 x LM48	151 00	266 87	27 09	25 92	0 80	115 87	208 94	200 74	0 42	0 57	0 49	192 87	0 43
37	LM47 x LM70	151 28	176 44	38 46	24 38	0 26	25 17	163 86	163 38	0 28	0 86	0 49	162 89	0 14
38	LM47 x LM71	89 96	350 05	31 15	27 94	1 36	260 10	220 00	177 45	0 33	0 26	0 29	143 13	0 74
39	LM47 x LM75	127 82	296 19	31 35	33 94	1 04	168 37	212 01	194 58	0 39	0 43	0 41	178 58	0 57
40	LM48 x LM70	124 35	379 95	59 07	18 41	1 24	255 60	252 15	217 36	0 49	0 33	0 40	187 37	0 67
41	LM48 x LM71	102 69	456 72	82 97	36 43	1 42	354 03	279 71	216 57	0 49	0 22	0 33	167 68	0 78
42	LM48 x LM75	125 23	397 27	21 65	25 69	1 26	272 04	261 25	223 05	0 52	0 32	0 40	190 43	0 68
43	LM70 x LM71	131 30	266 99	64 86	22 67	0 93	135 69	199 14	187 23	0 36	0 49	0 42	176 03	0 51
44	LM70 x LM75	151 73	452 21	29 55	47 30	1 22	300 48	301 97	261 94	0 71	0 34	0 49	227 22	0 66
45	LM71 x LM75	142 45	480 24	38 42	43 39	1 29	337 79	311 34	261 55	0 71	0 30	0 46	219 72	0 70

Y<sub>s</sub> = yield under drought-stressed conditions, Y<sub>p</sub> = yield under non-stressed conditions, RB<sub>s</sub> = root biomass under drought-stressed conditions, RB<sub>p</sub> = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

Appendix 5.2 continued

Entry	Genotypes	Y <sub>s</sub>	Y <sub>p</sub>	RB <sub>s</sub>	RB <sub>p</sub>	SSI	TOL	MP	GMP	STI	YSI	YI	HM	DSI
<b>Reciprocal crosses</b>														
46	BW141 x BW140	100 01	233 34	27 37	24 59	1 05	133 34	166 68	152 76	0 24	0 43	0 32	140 01	0 57
47	BW152 x BW140	118 60	357 41	53 34	23 31	1 23	238 81	238 01	205 89	0 44	0 33	0 38	178 10	0 67
48	BW152 x BW141	181 52	255 81	65 07	28 12	0 53	74 29	218 66	215 48	0 48	0 71	0 59	212 35	0 29
49	BW162 x BW140	158 99	252 10	57 73	16 06	0 68	93 10	205 55	200 21	0 42	0 63	0 51	195 00	0 37
50	BW162 x BW141	138 78	371 60	43 27	75 71	1 15	232 82	255 19	227 09	0 54	0 37	0 45	202 09	0 63
51	BW162 x BW152	130 49	297 69	32 65	53 62	1 03	167 20	214 09	197 09	0 40	0 44	0 42	181 45	0 56
52	LM26 x BW140	241 33	267 10	54 92	27 20	0 18	25 77	254 21	253 89	0 67	0 90	0 78	253 56	0 10
53	LM26 x BW141	165 70	347 67	21 70	37 95	0 96	181 97	256 68	240 02	0 60	0 48	0 53	224 43	0 52
54	LM26 x BW152	117 46	441 14	27 50	44 96	1 35	323 67	279 30	227 64	0 54	0 27	0 38	185 53	0 73
55	LM26 x BW162	149 85	374 41	50 50	34 58	1 10	224 56	262 13	236 87	0 58	0 40	0 48	214 04	0 60
56	LM47 x BW140	171 01	296 05	54 99	24 29	0 78	125 04	233 53	225 01	0 53	0 58	0 55	216 79	0 42
57	LM47 x BW141	115 28	265 43	73 29	31 28	1 04	150 15	190 35	174 92	0 32	0 43	0 37	160 74	0 57
58	LM47 x BW152	204 99	209 51	53 94	13 29	0 04	4 52	207 25	207 24	0 45	0 98	0 66	207 23	0 02
59	LM47 x BW162	99 36	225 81	36 82	41 11	1 03	126 45	162 59	149 79	0 23	0 44	0 32	138 00	0 56
60	LM47 x LM26	135 81	449 20	28 92	51 35	1 28	313 39	292 50	246 99	0 63	0 30	0 44	208 56	0 70
61	LM48 x BW140	177 98	465 86	32 60	48 37	1 13	287 88	321 92	287 94	0 86	0 38	0 57	257 56	0 62
62	LM48 x BW141	136 32	234 61	24 30	39 73	0 77	98 29	185 46	178 83	0 33	0 58	0 44	172 44	0 42
63	LM48 x BW152	124 07	274 34	28 29	50 77	1 01	150 27	199 21	184 49	0 35	0 45	0 40	170 87	0 55
64	LM48 x BW162	164 01	305 60	44 14	11 01	0 85	141 59	234 81	223 88	0 52	0 54	0 53	213 46	0 46
65	LM48 x LM26	149 02	362 82	49 37	26 10	1 08	213 80	255 92	232 52	0 56	0 41	0 48	211 27	0 59
66	LM48 x LM47	130 04	235 58	30 80	26 80	0 82	105 54	182 81	175 03	0 32	0 55	0 42	167 58	0 45
67	LM70 x BW140	141 96	197 30	17 02	45 10	0 51	55 34	169 63	167 36	0 29	0 72	0 46	165 12	0 28
68	LM70 x BW141	196 52	340 52	30 77	27 72	0 78	144 01	268 52	258 69	0 70	0 58	0 63	249 21	0 42
69	LM70 x BW152	202 60	350 53	40 57	15 19	0 77	147 93	276 56	266 49	0 74	0 58	0 65	256 78	0 42
70	LM70 x BW162	180 73	223 02	53 36	26 08	0 35	42 29	201 87	200 76	0 42	0 81	0 58	199 66	0 19
71	LM70 x LM26	172 00	194 95	54 35	15 81	0 22	22 95	183 47	183 11	0 35	0 88	0 55	182 75	0 12
72	LM70 x LM47	154 45	374 15	36 80	28 72	1 08	219 70	264 30	240 39	0 60	0 41	0 50	218 65	0 59
73	LM70 x LM48	116 67	271 77	12 15	10 03	1 05	155 10	194 22	178 06	0 33	0 43	0 38	163 25	0 57
74	LM71 x BW140	158 42	295 56	28 99	31 23	0 85	137 14	226 99	216 39	0 49	0 54	0 51	206 28	0 46
75	LM71 x BW141	122 44	250 02	45 84	23 11	0 94	127 58	186 23	174 97	0 32	0 49	0 39	164 38	0 51
76	LM71 x BW152	130 41	227 61	34 45	21 24	0 78	97 19	179 01	172 29	0 31	0 57	0 42	165 82	0 43
77	LM71 x BW162	104 44	362 54	30 87	31 60	1 31	258 10	233 49	194 58	0 39	0 29	0 34	162 16	0 71
78	LM71 x LM26	164 94	497 95	50 42	41 80	1 23	333 01	331 44	286 59	0 85	0 33	0 53	247 80	0 67
79	LM71 x LM47	115 09	276 88	28 76	26 54	1 07	161 80	195 99	178 51	0 33	0 42	0 37	162 59	0 58
80	LM71 x LM48	99 13	379 90	40 68	58 69	1 36	280 76	239 51	194 06	0 39	0 26	0 32	157 23	0 74
81	LM71 x LM70	127 13	233 06	41 87	18 28	0 83	105 94	180 10	172 13	0 31	0 55	0 41	164 52	0 45
82	LM75 x BW140	158 77	335 23	47 17	30 43	0 97	176 46	247 00	230 70	0 55	0 47	0 51	215 48	0 53
83	LM75 x BW141	184 58	345 85	28 82	33 32	0 86	161 27	265 21	252 66	0 66	0 53	0 60	240 70	0 47
84	LM75 x BW152	163 14	403 83	41 28	31 95	1 09	240 69	283 49	256 68	0 69	0 40	0 53	232 40	0 60
85	LM75 x BW162	144 82	314 11	30 00	33 09	0 99	169 29	229 47	213 29	0 47	0 46	0 47	198 25	0 54
86	LM75 x LM26	101 69	396 20	30 51	26 17	1 36	294 51	248 95	200 72	0 42	0 26	0 33	161 84	0 74
87	LM75 x LM47	177 73	304 43	37 59	28 09	0 76	126 70	241 08	232 61	0 56	0 58	0 57	224 44	0 42
88	LM75 x LM48	157 01	282 93	52 55	24 20	0 82	125 92	219 97	210 77	0 46	0 55	0 51	201 95	0 45
89	LM75 x LM70	154 74	232 17	17 56	28 18	0 61	77 43	193 46	189 54	0 37	0 67	0 50	185 71	0 33
90	LM75 x LM71	72 11	336 71	73 42	46 38	1 44	264 61	204 41	155 82	0 25	0 21	0 23	118 78	0 79

Y<sub>s</sub> = yield under drought-stressed conditions, Y<sub>p</sub> = yield under non-stressed conditions, RB<sub>s</sub> = root biomass under drought-stressed conditions, RB<sub>p</sub> = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

Appendix 5.2 continued

Entry	Genotypes	Y <sub>s</sub>	Y <sub>p</sub>	RB <sub>s</sub>	RB <sub>p</sub>	SSI	TOL	MP	GMP	STI	YSI	YI	HM	DSI
<b>Parents</b>														
<b>91</b>	BW140	131.38	353.33	42.47	27.62	1.15	221.95	242.36	215.45	0.48	0.37	0.42	191.54	0.63
<b>92</b>	BW141	145.66	194.97	23.32	15.23	0.46	49.31	170.32	168.52	0.30	0.75	0.47	166.75	0.25
<b>93</b>	BW152	67.00	420.74	23.24	31.00	1.54	353.74	243.87	167.90	0.29	0.16	0.22	115.60	0.84
<b>94</b>	BW162	152.67	373.88	28.12	26.75	1.09	221.21	263.28	238.92	0.59	0.41	0.49	216.81	0.59
<b>95</b>	LM26	137.19	312.63	28.51	17.21	1.03	175.44	224.91	207.10	0.45	0.44	0.44	190.70	0.56
<b>96</b>	LM47	88.92	310.53	32.64	22.85	1.31	221.60	199.73	166.17	0.29	0.29	0.29	138.26	0.71
<b>97</b>	LM48	100.27	228.59	21.78	13.73	1.03	128.32	164.43	151.40	0.24	0.44	0.32	139.40	0.56
<b>98</b>	LM70	118.71	396.39	42.40	19.11	1.29	277.68	257.55	216.93	0.49	0.30	0.38	182.71	0.70
<b>99</b>	LM71	100.87	241.39	28.57	36.02	1.07	140.52	171.13	156.05	0.25	0.42	0.33	142.29	0.58
<b>100</b>	LM75	267.32	335.78	70.25	49.96	0.37	68.46	301.55	299.60	0.93	0.80	0.86	297.67	0.20

Y<sub>s</sub> = yield under drought-stressed conditions, Y<sub>p</sub> = yield under non-stressed conditions, RB<sub>s</sub> = root biomass under drought-stressed conditions, RB<sub>p</sub> = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

Appendix 5.3. Grain yield, root biomass and drought-tolerance indices for the top drought-tolerant families and five most drought susceptibility families based on STI and GMP

Genotypes	Ys	Yp	RBs	RBp	GMP	STI	SSI	TOL	MP	YSI	YI	HM	DSI
<b>Drought tolerant families</b>													
<b>LM48 x BW140</b>	177.98	465.86	32.60	48.37	287.94	0.86	1.13	287.88	321.92	0.38	0.57	257.56	0.62
<b>BW162 x LM75</b>	188.96	436.16	64.09	37.16	287.08	0.86	1.04	247.20	312.56	0.43	0.61	263.69	0.57
<b>LM71 x LM26</b>	164.94	497.95	50.42	41.80	286.59	0.85	1.23	333.01	331.44	0.33	0.53	247.80	0.67
<b>LM70 x BW152</b>	202.60	350.53	40.57	15.19	266.49	0.74	0.77	147.93	276.56	0.58	0.65	256.78	0.42
<b>BW152 x LM75</b>	164.10	418.63	32.87	44.54	262.10	0.71	1.12	254.53	291.37	0.39	0.53	235.78	0.61
<b>LM70 x LM75</b>	151.73	452.21	29.55	47.30	261.94	0.71	1.22	300.48	301.97	0.34	0.49	227.22	0.66
<b>LM71 x LM75</b>	142.45	480.24	38.42	43.39	261.55	0.71	1.29	337.79	311.34	0.30	0.46	219.72	0.70
<b>LM26 x LM75</b>	141.50	481.21	53.31	40.12	260.94	0.71	1.30	339.71	311.36	0.29	0.46	218.70	0.71
<b>LM70 x BW141</b>	196.52	340.52	30.77	27.72	258.69	0.70	0.78	144.01	268.52	0.58	0.63	249.21	0.42
<b>LM75 x BW152</b>	163.14	403.83	41.28	31.95	256.68	0.69	1.09	240.69	283.49	0.40	0.53	232.40	0.60
<b>Drought susceptible families</b>													
<b>BW141 x LM71</b>	119.20	199.13	18.39	20.55	154.06	0.25	0.74	79.93	159.16	0.60	0.38	149.13	0.40
<b>BW141 x BW140</b>	100.01	233.34	27.37	24.59	152.76	0.24	1.05	133.34	166.68	0.43	0.32	140.01	0.57
<b>LM47 x BW162</b>	99.36	225.81	36.82	41.11	149.79	0.23	1.03	126.45	162.59	0.44	0.32	138.00	0.56
<b>BW140 x LM48</b>	137.40	151.68	23.04	7.14	144.37	0.22	0.17	14.28	144.54	0.91	0.44	144.19	0.09
<b>BW162 x LM70</b>	112.73	176.69	39.68	13.59	141.13	0.21	0.66	63.96	144.71	0.64	0.36	137.65	0.36

Ys = yield under drought-stressed conditions, Yp = yield under non-stressed conditions, RBs = root biomass under drought-stressed conditions, RBp = root biomass under non-stressed conditions, GMP = geometric mean productivity, STI = stress tolerance index, SSI = stress susceptibility index, TOL = tolerance index, MP = mean productivity, YSI = yield stability index, YI = yield index, HM = harmonic mean, DSI = drought susceptibility index

## General Overview and Implications for Breeding

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Bread wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ , AABBDD) is a vital global commodity crop with well-defined value chains. Recurrent drought and erratic rainfall conditions due to climate change threaten sustainable wheat production. Developing wheat varieties that are more tolerant to drought and are better adapted to an ever-changing climate will be key in enhancing food security. Some crop genotypes increase biomass allocation to the root system as stress adaptation mechanism, a trait that can be selected in crop breeding programs. Increased root biomass and sizes improve access to water deeper in the soil profile for drought avoidance. In addition, the increased allocation of plant biomass to the roots may contribute more carbon and nutrients into soils through root activity and root decay, ultimately turning into soil organic matter. This will reduce soil degradation from agricultural practices and improve soil health for more sustainable and resilient wheat agro-ecosystems.

This chapter summarizes the research objectives and findings of this study and identifies areas for future research. The specific objectives of this study were:

- i. to provide information based on a retrospective quantitative genetic analysis on combining ability studies of wheat for yield and yield-related traits to predict potential genetic gains achievable in improving biomass allocation for drought tolerance and soil carbon storage;
- ii. to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents;
- iii. to estimate the magnitude of the relationship between root biomass and yield components and to identify influential traits to optimise genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat (*Triticum aestivum* L.);
- iv. to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat to identify good combiners for breeding and enhanced carbon sequestration, and;

- v. to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement.

### **A meta-analysis of combining ability effects in wheat for agronomic traits and drought adaptation: implications for optimizing biomass allocation**

Meta data were assembled and analysed on the general combining ability (GCA) and specific combining ability (SCA) effects of wheat populations involving 40 studies worldwide. Data on the GCA and SCA effects of the following traits were recorded: days to heading (DTH), plant height (PH), productive tiller number (TN), kernels per spike (KPS), thousand kernel weight (TKW), shoot biomass (SB) and grain yield (GY) under optimum and drought stressed conditions. Summary statistics, Pearson's correlation coefficients, principal component analysis and meta effects were calculated. The major findings of the study were as follows:

- Progeny performance increased for SB and GY compared with parental values under optimum water conditions.
- Positive associations with GY were observed for TN and SB under drought-stressed and non-stressed conditions.
- The highest meta-effect sizes for drought were for DTH followed by SB, while KPS had the lowest.
- The genetic gains for PH, SB and other yield components showed that divergent crosses involving complementary parents could enhance biomass allocation patterns in wheat.

### **Comparative genetic diversity analysis for biomass allocation and drought tolerance in wheat**

Ninety-seven bread wheat genotypes were evaluated in three separate experiments conducted under drought-stressed and non-stressed conditions and genotyped using 16,382 SNP markers based on the DArT-seq protocol. Data on days to 50% heading, days to 50% maturity (DTM), plant height, productive tiller number, total plant biomass (PB), shoot biomass, root biomass (RB), root-to-shoot ratio (RS) and grain yield were recorded. The main findings were as follows:

- Principal component analysis revealed that PB, SB, RB and GY explained most of the variation among the genotypes under drought-stressed and non-stressed conditions.

- Genetic parameters varied widely. The genetic distance, polymorphic information content and expected heterozygosity ranged from 0.20 to 0.88, 0.24 to 1.00 and 0.29 to 0.58, respectively.
- The cluster analysis based on SNP data showed that 44% and 28% of the assessed genotypes maintained their genetic groups compared to hierarchical clusters under drought-stressed and non-stressed phenotypic data, respectively.
- Analysis using genotypic and phenotypic data resolved three heterotic groups enabling the selection of desirable parents for combining ability analysis.

### **Path coefficient and principal component analyses for biomass allocation, drought tolerance and carbon sequestration potential in wheat**

Ten selected parents and 90 F<sub>2</sub> families, including direct and reciprocal crosses, were evaluated under drought-stressed and non-stressed conditions. Data were collected for DTH, DTM, PH, TN, spike length (SL), spikelets per spike (SPS), KPS, TKW, SB, RB, PB, RS and GY. The main findings were as follows:

- There was no significant genetic variation for RS and TN.
- Significant positive correlations were observed for RB and SB under both water regimes, revealing the potential of increasing both traits with minimal biomass trade-offs.
- The highest positive direct effects on grain yield were found for KPS and PB under drought-stressed and non-stressed conditions.
- Selection based on KPS and PB rather than RS will be more effective in ideotype selection of segregating populations for drought tolerance and carbon sequestration potential.

### **Genetic analysis of yield and yield-related traits and biomass allocation in newly developed wheat populations**

The above data for PH, KPS, RB, SB, PB and GY were subjected to combining ability analysis of to determine the maternal effects and the mode of gene action controlling the major yield-related traits and biomass production to identify good parents and progenies for breeding. The main outcomes of the study were as follows:

- Additive gene effects conditioned PH, SB, PB and GY under drought, suggesting the polygenic inheritance for drought tolerance.
- Strong maternal and reciprocal genetic effects were recorded for RB across the testing sites under drought-stressed conditions.
- Parental line LM75 maintained GCA effects in a positive and desirable direction for SB, PB and GY.
- Reciprocal crosses LM47 × BW152, LM26 × BW140 and LM75 × LM47 had significant reciprocal effects on root biomass and grain yield and should be considered for forward selection.

### **Advancing grain yield, drought adaption and biomass allocation in wheat populations**

The new families and their parents involved in the above crosses were evaluated in a 10 × 10 alpha alpha-lattice design under field and greenhouse conditions. Data on PH, KPS, RB, SB, PB and GY were collected to determine the genetic variability, heritability and genetic advance. The main findings of the study were as follows:

- Heritability estimates under drought-stressed conditions were moderate for PH (50.33%) and RB (41.61%); and low for GY (18.79%).
- Geometric mean productivity (GMP) and stress tolerance index (STI) were the most efficient drought-tolerance indices for selecting drought-tolerant families with high RB.
- Direct crosses BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 are recommended for genetic advancement.

### **Implications for breeding drought-tolerant wheat with high biomass production**

- The global meta-analysis showed sufficient genetic variation for above-ground traits to improve productivity and biomass allocation between roots and shoots in wheat for food production and ecosystem services such as nutrient recycling and carbon retention. Therefore, optimising total biomass allocation in new wheat genotypes will be essential to withstand the adverse effects of drought while maintaining soil health by retaining biomass for carbon sequestration.

- Considerable genetic variation was available in the panel of wheat genotypes evaluated in this study. However, it is recommended that genetic diversity analysis be done in more diverse environments to capture the variation due to the genotype-environment interaction effect and increase the repeatability of data gathered from phenotypic and molecular parameters. In addition, landraces, older varieties, and obsolete cultivars should be used strategically in breeding programs to introgress genes for root system traits that may be absent in elite wheat genotypes.
- The positive relationship between RB and SB informs the possibility of increasing both traits with minimum biomass trade-offs to develop drought-tolerant cultivars with high carbon sequestration potential. Therefore, indirect selection using KPS and PB will be more efficient for improving grain yield under different soil moisture conditions while pursuing the goal of increasing carbon inputs in wheat production systems.
- Selection using PH, SB, PB and GY is recommended to improve drought tolerance by exploiting additive gene action controlling these traits under drought conditions. Genetic gains may be achieved for RB by positive selection of male and female parents to capture the significant maternal and reciprocal effects during hybridization.
- Overall, the study identified new families with enhanced drought tolerance and high biomass production. The identified families should be advanced for cultivar development and further evaluated for net carbon contribution to the soil.