Early Generation Selection of Bread Wheat (*Triticum aestivum* L.) Genotypes for Drought Tolerance

By

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A dissertation submitted in partial fulfilment of the requirements for the degree of Master of Science (MSc) in Plant Breeding

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Republic of South Africa

November 2018

Dissertation Abstract

Wheat (*Triticum aestivum* L.) is the third most important cereal crop after rice and maize globally. Dryland wheat production in South Africa is challenged by recurrent drought leading to low profitability for farmers. Development of drought tolerant wheat genotypes presents the most sustainable strategy to mitigate the effects of drought stress associated with climate change. In an attempt to develop drought tolerant wheat genotypes, the wheat research group at the University of KwaZulu-Natal (UKZN) in collaboration with the Agricultural Research Council-Small Grain Institute (ARC-SGI) developed a breeding population and advanced it to the F_2 generation. The breeding population was developed through crosses involving selected promising parents with local drought susceptible cultivars. The F_2 families need to be advanced to the F_3 generation and selected for genetic advancement with regards to drought tolerance and important agronomic traits. Therefore, the overall objective of this study was to select superior drought tolerant bread wheat families at the F_3 generation for further screening in advanced generations. The specific objectives of the study were: 1) to undertake early generation selection of wheat genotypes for drought tolerance and agronomic traits for genetic advancement, 2) to determine the combining ability effects and the mode of gene action that controls yield and yield components in selected wheat genotypes under drought-stressed and non-stressed conditions, and 3) to assess the association between yield and yield-components in wheat and identify the most important components to improve grain yield and drought tolerance.

Seventy-eight genotypes consisting of 12 parents and their 66 F_3 families were evaluated using a 13 x 6 alpha-lattice design with two replications in two contrasting water regimes under greenhouse and field conditions in the 2017/2018 growing season. The following agronomic traits were assessed: number of 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), fresh biomass (BI) and grain yield (GY). Highly significant differences ($P<0.05$) were observed for the assessed traits among the genotypes under the two water regimes. Variance components and heritability estimates among agronomic traits and yield showed high values for days to heading and fresh biomass under drought stress. Genetic advance values of 29.73% and 37.61% were calculated under drought-stressed and non-stressed conditions, respectively, for fresh biomass. The families LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 were relatively high yielding in both stressed and non-stressed conditions and are recommended for genetic advancement.

The above data were subjected to combining ability analysis to discern best combiners. Significant general combining ability (GCA) effects of parents were observed for DTH, PH and

SL in both the greenhouse and the field under drought-stressed and non-stressed conditions. The specific combining ability (SCA) effects of progenies were only significant for DTH under all testing conditions. The heritability of most traits was low ($0 < h^2 < 0.40$) except for SL which showed moderate heritability of 0.41 under drought-stressed condition. The GCA/SCA ratio was below one for all the traits indicating the predominance of non-additive gene action. Low negative GCA effects were observed for DTH, DTM and PH on parental line LM17 in a desirable direction for drought tolerance. High positive GCA effects were observed on LM23 for TN and SL, LM04 and LM05 (for SL, SPS and KPS), LM21 (TKW), LM13 and LM23 (BI) and LM02, LM13 and LM23 for GY. Families LM02 x LM05 and LM02 x LM17 were the best performers across the test conditions.

Significant correlations (P<0.05) were observed between GY with PH, TN, SL, KPS, TKW and BI under both drought-stressed and non-stressed conditions. Partitioning of correlation coefficients into direct and indirect effects revealed high positive direct effects of KPS and BI on GY under drought-stressed conditions. Among all the assessed traits, BI had significant simple correlations of 0.75 and 0.90, and high direct effects of 0.76 and 0.98 with grain yield under drought-stressed and non-stressed conditions, in that order. The top yielding genotypes such as LM02 x LM05, LM02 x LM23 and LM13 x LM45, showed high mean values for KPS, TKW and BI. The overall association analyses indicated that the latter three traits had significant influence on grain yield performance and are useful for selection of drought tolerant breeding populations of wheat.

Overall, the present study identified promising families including LM02 x LM05, LM02 x LM23, LM09 x LM45 and LM13 x LM45 that have drought tolerance and suitable agronomic traits. These families can be advanced using the single seed descent selection method for further characterisation of end-use quality traits and comparison with local checks or commercial cultivars.

Declaration

1. I, Kwame Wilson Shamuyarira, declare that:
2. The research reported in this dissertation, except where otherwise indicated is my original research.
3. This dissertation has not been submitted for any degree or examination at any other university.
4. This dissertation does not contain other persons data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
5. This dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
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Signed

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Kwame Wilson Shamuyarira

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

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Prof. Hussein Shimelis (Supervisor)

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Prof. Toi J. Tsilo (Co-Supervisor)

Acknowledgements

- First of all, I would like to thank Prof. Hussein Shimelis, my supervisor, for the advice and guidance in this entire research. You taught me the need to pay attention to details and to aim for excellence in my research.
- I would like to thank Prof. Toi Tsilo for his advice and support which were critical in the carrying out of this research.
- This work would not have been possible without the financial support of the National Research Foundation (NRF) through the Agricultural Research Council-Small Grain Institute (ARC-SGI) which is sincerely appreciated.
- I am heavily indebted to Dr. Learnmore Mwadzingeni who was a regular guide in every aspect from the beginning to the end of this research which would not have come to completion without his guidance and support.
- Sincere thanks and respects go to Dr. Terence Tapera for his assistance in data analysis and review of manuscripts which were essential in improving the output of this research.
- I would like to thank the African Centre for Crop Improvement (ACCI) technical staff including Mr. Ian Doidge, Mrs. Susan Van der Merwe and Mr. Shadreck Munatsi for their assistance during field and greenhouse experiments.
- I am grateful to Mrs. Rowelda Donelly and Mrs. Lyndre Anderson for their administrative support through the entire research period.
- I would like to extend my deepest gratitude to Dr. Cousin Musvosvi, Isack Mathew, Admire Shayanowako, Marylyn Christian and Sibusiswangaye Mdluli for their motivation which kept me going.
- A heartfelt thanks go to the 2017 ACCI and AGRA cohort for their support in difficult moments and the experiences that we shared together. Special thanks go to Happy Daudi for all her assistance.
- Finally, I want to thank my parents for their love, dedication and support through this research. Most importantly, I thank God who has always been a constant guide and protector in my life.

Dedication

This work is dedicated to the wheat farmers in the dryland regions of South Africa, with a hope that one day drought tolerance work documented in this dissertation will benefit them.

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Abbreviations

ARC-SGI	Agricultural Research Council-Small Grain Institute
BI	Fresh biomass
CIMMYT	International Maize and Wheat Improvement Center
CV	Coefficient of variation
DTH	Days to heading
DTM	Days to maturity
ENSO	El Nino Southern Oscillation
GA	Genetic advance
GAM	Genetic advance as percentage of mean
GCA	General combining ability
GCV	Genotypic coefficient of variation
GY	Grain yield
H^2	Broad sense heritability
KPS	Kernels per spike
LSD	Least significant difference
PCV	Phenotypic coefficient of variation
PH	Plant height
QTL	Quantitative trait loci
SCA	Specific combining ability
SL	Spike length
SPS	Spikelets per spike
SSA	Sub-Saharan Africa
TKW	Thousand kernel weight

TN	Productive tiller number
UKZN	University of KwaZulu-Natal

Introduction to Dissertation

Background of study

Wheat (*Triticum aestivum* L., AABBDD, 2n = 6x = 42) is the third most important staple cereal crop after maize (*Zea mays* L.) and rice (*Oryza sativa* L.) vital for global economies (Cakmak et al., 2017). Wheat provides approximately 20% of the carbohydrate and protein requirement of the world's population (Flister and Galushko, 2016). The global significance of wheat is attributed to its market share in the value chains of diverse food and industrial products (Fones and Gurr, 2015). Population growth and rapid urbanization is likely to reduce agricultural lands for crop production. This implies that to meet the global demand for wheat, higher productivity is expected on a relatively small land area using high performing and quality wheat varieties that meet market demands (Alexander et al., 2015).

The level of wheat production in sub-Saharan Africa (SSA) is low or steadily declining. Consequently, regional demands for wheat is met through substantial imports (Negassa et al., 2013). The mean wheat yields in SSA average 2.0 t/ha compared with the potential yield of the crop reaching up to 10 t/ha (Negassa et al., 2013; Dube et al., 2018). The yield gap in SSA is attributed to an array of production constraints such as drought and heat stress, poor agronomic management practices, pests and diseases and unavailability of improved varieties (Waddington et al., 2010). In South Africa, wheat production has declined due to increased drought incidence associated with climate change (Dube et al., 2016). The impact of recurrent droughts will continue to influence wheat production in South Africa and other countries in SSA.

Drought stress is the major constraint to wheat productivity in dryland regions of South Africa (Dube et al., 2016). It is projected that due to climate change, drought duration and severity will continue to increase and affect crop production and productivity in dryland areas (Nezhadahmadi et al., 2013; Schlaepfer et al., 2017). Drought affects the growth process and development of wheat during the entire crop cycle (Vurukonda et al., 2016). However, wheat is highly sensitive to drought stress during anthesis to grain filling stages (Farooq et al., 2014). Yield losses at these stages are associated with reduced grain number and weight. According to Griffiths et al. (2015), grain number and grain weight are the two most important parameters that determine the final grain yield in wheat. Drought occurrence during anthesis reduces development of floral structures causing pollen sterility and delaying initiation of grain formation resulting in poor grain set (Dong et al., 2017). During grain filling, drought decreases transportation of photo-assimilates to the young grain leading to poorly formed and shrivelled grain (Farooq et al., 2015). Therefore, to limit yield reduction due to terminal drought stress, adoption of drought tolerant cultivars is a vital component of dryland wheat production.

Drought tolerant wheat genotypes enhance grain yield productivity under dryland production systems. Drought tolerance is a polygenic trait influenced by many minor genes (Budak et al., 2015). The occurrence, intensity and duration of drought is subject to genotype x environment interaction necessitating selection for drought tolerant genotypes across representative test environments (Langridge and Reynolds, 2015). For successful development and deployment of drought tolerant genotypes, promising wheat genetic resources that possess adequate genetic variation for drought tolerance must be available to breeders (Jansky et al., 2015). Centers of diversity and gene banks are excellent sources for germplasm collection for germplasm that can be used in plant breeding programs (Ghimiray and Vernooy, 2017). In the case of wheat, the International Maize and Wheat Improvement Centre (CIMMYT) holds the largest wheat germplasm collection and targets development of drought tolerant germplasm that is accessible globally to plant breeders (Manes et al., 2012).

Evaluation of germplasm collected from gene banks under local conditions is necessary to identify genotypes that will be valuable for local breeding programs (Mwadzingeni et al., 2016a). After evaluation, selected genotypes are subjected to genetic analysis to determine their usefulness in developing locally adapted drought tolerant lines. To determine their genetic value, selected genotypes can be crossed using a suitable mating design and evaluated based on the performance of their progenies. Diallel analysis is the most suitable mating design for estimating the general combining ability (GCA) of parental lines and specific combining ability (SCA) of families obtained from crosses (Jocic et al., 2015). The combining ability estimates are essential in identifying the best parents that can be used in well-designed crosses to develop drought tolerant lines. Furthermore, the diallel mating design is useful in assessing the nature and magnitude of gene action for complex traits such as drought tolerance (Musembi et al., 2015).

Information on combining ability and gene action is valuable in determining the selection strategy involving crosses and families. In plant breeding of self-pollinating crops including wheat, early generation selection is a selection strategy that is valuable in minimizing costs associated with advancing many breeding populations. Early generation selection involves selection of highly performing families during the F_3 to F_5 generations for genetic advancement (Clement et al., 2015). This method limits the loss of valuable genes present in superior families at advanced generations (Singh and Sharma, 2016). The success of early generation selection is dependent on the presence of additive gene action for targeted traits (Fasahat et al., 2016). Early generation selection is achieved by selection of families obtained from crosses of good general combiners which indicate prevalence of additive gene action (Singh et al., 2016). In addition, the traits of interest should be highly heritable and have a high selection response for effective selection (Ahmad et al., 2017). Conversely, the presence of non-additive gene action indicates non-fixable genetic variation and selection will need to be delayed to advanced generations (Hussain et al., 2017).

Grain yield remains the target trait for selection to improve drought tolerance in wheat. Typically, an ideal wheat cultivar should possess high yield potential that is acceptable to the farmer and value chains (Ataei et al., 2017). Yet, yield is influenced by many agronomic traits and yield components that are inter-related and have different contributions to final grain yield. As such, Abdolshahi et al. (2015) identifies indirect selection for grain yield using yield components as the most efficient way to increase productivity under drought stress. Assessing yield components aids in identifying the key traits that influence yield under drought stress and simplifies selection of drought tolerant genotypes (Senapati et al., 2018).

Yield components have a direct or indirect influence on grain yield. Therefore, identification of the direct and indirect effects of traits increases the selection efficiency in wheat breeding programs (Shukla et al., 2015). Simple correlation analysis and path coefficient analysis are techniques that can be used to determine trait associations. Employing both techniques in selection for drought tolerance will hasten genetic improvement through targeted selection of key traits. According to Silva et al. (2016), use of correlated traits with high heritability values increases genetic gains in plant breeding programs. Several reports indicate that major yield increases in different regions globally has been a result of the increase of a few components that were correlated to grain yield (Qin et al., 2015; Mansouri et al., 2018; Valvo et al., 2018). Therefore, use of different selection strategies and techniques to develop drought tolerant wheat genotypes offers the most sustainable option to increase wheat productivity in South African dryland regions.

Rationale of study

Wheat in South Africa is the second most important cereal crop after maize in terms of both agricultural land area coverage and harvestable yields (Nalley et al. 2018). Wheat production in dryland regions of South Africa is mostly under low agricultural input systems which are highly constrained with recurrent droughts worsened by increasing variability of precipitation patterns due to climate change. As a result, South African wheat productivity has declined over the years due to drought stress in dryland growing areas, among other production constraints. Breeding for drought tolerance is one of the sustainable measures that can be adopted to increase crop production levels under both marginal and optimum moisture conditions. In response to this need, the Agricultural Research Council - Small Grains Institute (ARC-SGI) initiated a wheat breeding program involving initial germplasm collection of drought tolerant wheat lines from CIMMYT. This material underwent rigorous selection for drought tolerance using phenotypic traits and proline analysis (Mwadzingeni et al., 2016b). The population structure and association mapping of the same material was conducted to identify genetic markers for use in marker-assisted selection (Mwadzingeni et al., 2017). Twelve genotypes were selected and crossed using a half-diallel mating design to produce F_1 families which were advanced to F_2 generation for combining ability analysis (Mwadzingeni et al., 2018). The F_3 seeds obtained from Mwadzingeni et al. (2018) need to be subjected to continuous selection for variety recommendation and release. As part of this initiative, the present study subjected the F_3 lines to early generation selection for genetic advancement of promising lines to F_4 generation. Early generation selection is a selection strategy employed in plant breeding programs to identify promising genotypes for further genetic advancement and release. Early generation selection aids in reducing the cost of running plant breeding projects by considerably reducing the amount of genetic material handled in later generations.

Overall research objective

The study aimed to identify and select superior drought tolerant F_3 bread wheat families among available South African wheat germplasm for targeted genetic advancement at later generations.

Specific objectives

i. to undertake early generation selection of wheat genotypes for drought tolerance and agronomic traits for genetic advancement.
ii. to determine the combining ability effects and the mode of gene action that controls yield and yield components in selected wheat genotypes under drought-stressed and non-stressed conditions.
iii. to assess the association between yield and yield components in wheat and identify the most important components to improve grain yield and drought tolerance.

Hypotheses

i. Early generation selection is effective in identifying superior drought tolerant families for genetic advancement.
ii. Additive gene action is predominant in governing yield and yield components in wheat under drought-stressed and non-stressed conditions.

iii. Yield components are associated with grain yield in bread wheat under drought-stressed and non-stressed conditions.

Outline of dissertation

The dissertation consists of four chapters in accordance with the number of objectives (Table 0.1). The dissertation is written in the form of discrete 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 dissertation 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 dissertation is based on the Journal of Crop Science referencing system.

Table 0.1 Outline of dissertation

Chapter	Title
-	Introduction to dissertation
1	Literature review
2	Early generation selection of wheat genotypes for drought tolerance and agronomic traits
3	Combining ability analysis for yield and agronomic traits among F_3 lines of wheat under drought-stressed and non-stressed conditions
4	Correlation and path coefficient analyses of yield and yield-components in drought tolerant bread wheat populations
-	General conclusions and recommendations

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CHAPTER 1

Literature Review

Abstract

This review mainly focuses on highlighting the effect of biotic and abiotic stresses on wheat production and productivity. It emphasized on terminal drought stress and the response of wheat to drought stress. The review covers breeding methods that have been used to improve drought tolerance in wheat. It further discussed on the breeding strategies that can be employed to increase selection efficiency and genetic gains for drought tolerance in wheat. The application of early generation selection in improving selection efficiency is highlighted in the end.

Keywords: *Drought tolerance, early generation selection, heritability, terminal drought, wheat*

1.1 Introduction

Bread wheat (*Triticum aestivum* L, *2x=6x=42*, AABBDD) is an allopolyploid species that supports more than one billion people worldwide, both as a food and industrial crop (Xu et al., 2017). It belongs to the family Poaceae, and together with maize, rice, sorghum and barley it forms the most economically important cereal crops globally. The genus *Triticum* is genetically diverse and consists of different species, including durum wheat (*T. durum* Desf, *2n=4x=28*) and emmer wheat (*T. dicoccum* Schrank *ex* Schübler, *2n=4x=28*). Other wild relatives include the species *T. dicoccoides* and *Aegilopes tauschii*. Among these, bread wheat is the most widely cultivated constituting 95% of global wheat production followed by durum wheat which makes up the other 5% (Arzani and Ashraf, 2017). Bread wheat is mainly used to prepare bread, biscuits and cakes, whereas durum wheat is used for making pasta products (Pauly et al., 2013). Bread wheat is also used for industrial purposes where it is processed into starch and gluten to make natural adhesives, cosmetics, plastic films and processed food products such as pet food and aquaculture feed (Balandrán-Quintana et al., 2015). A very small proportion of wheat is used as animal feed with the amount being determined by the price of other feed grains (Carver, 2009).

Wheat species have different ploidy levels, which include diploid (2n=2x=14), tetraploid (2n=4x=28) and hexaploid (2n=6x=42) (Goncharov, 2005). Bread wheat is believed to be originated from hybridization between the tetraploid *T turgidum* (2n=4x=28, AABB) and *Ae. tauschii* (2n=14, DD) (Hirosawa et al., 2004; Salse et al., 2008; Brenchley et al., 2012). *Triticum turgidum* is in turn proposed to have been a product of hybridization between *T. urartu* (2n=14, AA), contributor of the AA genome and an unknown species, which was the contributor of the BB genome (Salse et al., 2008). In addition to its polyploid nature, *T. aestivum* has a large and complex genome size of 17 gigabase (Brenchley et al., 2012). This polyploid nature partially contributes to its wide adaptability to a wide range of climatic conditions, which has led to its success as a global food security crop (Marcussen et al., 2014).

1.2 Production and economic value of wheat

Wheat production is well distributed throughout the world with the major producing countries being China and India (Singh et al., 2017; Zulauf 2017). Global wheat production covers around 215 million hectares, with an annual production of around 630 million tonnes (Salim et al., 2017). Wheat production in Africa is low compared to other regions and is mainly concentrated in North Africa where it has historically been an important crop (Galati et al., 2014). The major producers of wheat in Africa include Egypt, Morocco, Ethiopia and South Africa (FAOSTAT, 2017)

The socio-economic value of wheat has increased in the last 50 years in sub-Saharan Africa (SSA) (Awika, 2011). The growth in the importance of wheat has been driven by several factors which include growing incomes, urbanization and the growing population in SSA (Mason et al., 2012). Its consumption is increasing at a faster rate in SSA than any other cereal or food grain (Mason et al., 2012). However, a very small area in Africa is yet used for wheat production (Ray et al., 2013). The per capita growth rate of wheat consumption in SSA is the highest in the world and wheat imports in the region are projected to increase by 23.1 million tons by 2050 (Weigand 2011). The rise in imports is mainly due to low wheat production levels in the region, which remain far below the demand for wheat and wheat products (Shiferaw et al., 2011). According to Gianessi (2014), 70% of the wheat consumed in SSA is imported at an annual cost of about US $5 billion dollars a year. Therefore, there is need for import substitution through regional production and trade.

1.3 Reproductive stages of wheat

The reproductive stage is one of the most important stages of plant development, which is essential for their survival and ability to reproduce (Kane et al., 2005). For reproduction to be successful, the initiation of the reproductive stage should occur when the environmental conditions are suitable for efficient reproduction (Kim et al., 2009). In wheat, the reproductive stage is very crucial because it has major impact on the final yield by determining the duration of spike formation and influencing the grain filling period (Royo et al., 2017). Spike development in wheat takes place inside the leaf sheath and once it is complete the spike emerges out of the leaf sheath (Gol et al., 2017). When the spike has emerged, the wheat plant will have entered its reproductive stage.

The initiation of reproduction in wheat is influenced mainly by two environmental factors which are temperature and day length (Reynolds et al., 1996). Therefore, these two factors are important in the adaptation of wheat to different environments and allow them to adjust and cope with unfavorable environments (Klaimi and Qualset, 1973). Wheat can be classified into two groups based on whether it requires vernalization for initiation of flowering or not. Vernalization is defined as "*the acquisition or acceleration of the ability to flower by a chilling treatment*" (Chouard, 1960). Plants that require a period of vernalization to flower are classed as winter wheat, whereas those that can flower without experiencing a cold spell are classed as spring wheat (Larsen, 2012). The vernalization temperatures required by winter wheat are proposed to be below 10^{o}C (Salunkhe and Deshpande, 2012). The duration of the cold spell is very important and should be long enough to ensure sufficient vernalization (Li et al., 2013). However, the duration of vernalization required varies among cultivars (Goncharov, 2004). Winter wheat is planted in autumn and develops to the tillering stage before it experiences winter temperatures, which induces vernalization, whereas the spring wheat is planted in summer after the risk of frost (Rincón et al., 2016).

Flowering plants can be classified into either long day plants or short-day plants depending on whether short or long days trigger the transition from the vegetative to the reproductive stage of growth (Brambilla et al., 2017). In wheat, flowering is hastened during longer days and delayed when days are short (Zhao et al., 2016). The effect of daylength on the flowering time in wheat differs greatly among cultivars and is dependent on the interaction of the genotype with the environment (Klaimi and Qualset, 1973; Zikhali et al., 2017). Sensitivity to photoperiod is high in some cultivars, which are termed "*photoperiod sensitive cultivars*" and low in "*photoperiod insensitive cultivars*" (Zhao et al., 2016).

Wheat is an autogamous species exhibiting about 1% cross pollination (Hucl and Matus-Cadiz, 2001; Singh et al., 2010), with some cultivars showing greater tendency to outcross than others (Waines and Hegde, 2003). The self-pollinating nature of wheat is brought about by its floral biology where the receptivity of the stigmas and the maturation of the pollen occur during the same period which ensures that the stigmas are usually pollinated by pollen from anthers within the floret (Gustafson et al., 2005). The wheat flower is also cleistogamous, delaying the protrusion of the anthers outside the floret and thus promoting self-fertilization (Muqaddasi et al., 2017). In addition, production of pollen in wheat is very low to allow high outcrossing, a common feature in self-pollinating crops, and is estimated to be about 2.5% that of a maize flower (De Vries, 1971).

1.4 Constraints to wheat production

1.4.1 Biotic stresses

There are a variety of challenges that wheat farmers face. Biotic stresses such as pests and diseases are a major problem to many wheat growers around the world. The occurrence of pests and diseases varies with some having a wide occurrence than others. Some cause serious damage to crop production, while others cause relatively minimal damage (McIntosh, 1997). Among these, the major stresses are fungal diseases including leaf rust, stem rust, stripe rust, kernel bunt, powdery mildew and spot blotch. (Kazi et al., 2013). Of all the diseases, the rusts have a global presence and are prevalent in regions that have warm and humid conditions (Figueroa, 2018). In Africa and the Middle East, the Ug99 race of stem rust is the most devastating and has caused large yield losses with major epidemics occurring in southern Ethiopia since 2013 (Zhang et al., 2017). Aphid species are also economically important pests and cause crop damage by either directly feeding on the plant or as vectors of plant viruses (Aradottir et al., 2017). In South Africa, the Russian Wheat Aphid is the most damaging and economically important pest especially in the summer rainfall areas (Botha et al., 2017). Of the viral diseases spread by aphids, barley yellow dwarf virus vectored by the wheat aphid *Sitobion avenae* is growing in importance (Tanguy and Dedryver, 2009; Kazi et al., 2013) especially in Central Europe (Honek et al., 2017) and China (Xin et al., 2014).

1.4.2 Abiotic stresses

Wheat is affected by several abiotic stresses, which reduce yield significantly. According to Cramer et al. (2011), abiotic stress can be defined as "*environmental conditions that reduce growth and yield below optimum levels*". These stresses include drought, salinity, poor soil nutrition, extreme temperatures and toxins introduced by human activity such as herbicides, chemical fertilizers and heavy metal build up in soils (Jenks and Hasegawa, 2008; Kumar, 2013). In a survey covering 19 developing countries including three in Africa, the major abiotic stresses that affected wheat production were heat stress and low rainfall (Kosina et al., 2007).

Heat stress greatly compromises the potential yield of wheat compared to other crops as it is generally cultivated as a winter crop in sub-Saharan Africa (Adhikari et al., 2015). Higher temperatures reduce the number of days to anthesis and maturation thus limiting the time that the plant can intercept light for photosynthesis leading to low production of photosynthetic assimilates required for grain filling (Asseng et al., 2015). According to Gibson and Paulsen (1999), high temperatures can decrease wheat yields by 3% to 5% per 1^{o}C increase in temperature above 15^{o}C for plants grown under controlled conditions. The intensity of the heat stress and the period of exposure to heat stress determines the level of damage on the development of the wheat crop. Extremely high temperatures and prolonged exposure to heat stress can cause permanent damage to the crop and yield loss (Zampieri et al., 2017). High temperatures also lead to increased levels of evapotranspiration, which induces or increases the severity of drought stress.

Water is an essential element involved in all metabolic processes of the plant and is required for normal plant growth and development (Shakirova et al., 2016). In agriculture, availability of enough soil moisture for crop growth during the growing season is critical to ensure optimum productivity. When available soil moisture diminishes below the water requirements of plants coupled with evapotranspiration rates that exceed the rate of water uptake, drought stress sets in (Jaleel et al., 2009). Thus, when drought stress occurs, plant growth and development is compromised.

The frequency and occurrence of drought events is set to increase in the future due to the effects of climate change (El-Hendawy et al., 2017). The impact of climate change is acknowledged as the major cause of the changing precipitation patterns in the world. Among the phenomenon impacting on climate change, the El Niño southern oscillation (ENSO) causes changes in climatic patterns globally (Chen and Tam, 2010). The ENSO has grown in influence over the last three decades and strong events have led to devastating effects on major cereal production due to decreased precipitation (Rosenzweig et al., 2001). Indirectly, less precipitation has impacted agricultural productivity by reducing water supply for irrigation purposes thereby increasing the severity of stress episodes on crop growth (Hao et al., 2015). As a result, semi-arid regions which already face critical water shortages remain the most vulnerable to increased incidence of drought stress (Nawaz et al., 2015).

Exposure of semi-arid regions in under-developed countries mainly in Africa and Asia to drought reduces production and profitability of crops such as wheat under dryland conditions (Daryanto et al., 2016). At the same time, due to increased demand, more food should be produced in the face of reduced water supplies and unpredictable precipitation patterns on deteriorating arable lands with poor and unproductive soils (Mickelbart et al., 2015). This presents a devastating picture of attempting to raise agricultural productivity under worsening moisture conditions. Therefore, the focus of this review is to discuss the effects of drought stress and how breeding drought tolerant cultivars can alleviate yield loss in wheat.

1.5 Drought stress

The negative impact of drought on crop production is extensive and affects many areas of the world (Nakashima and Suenaga, 2017). Drought is projected to increase the pressure on global food production than in the past (Daryanto et al., 2017). Yield is influenced by the variable levels of water deficit during the crops' development (Langridge and Reynolds, 2015). Drought affects crops at all stages of plant development by inhibiting crop growth, decreasing the rate of photosynthesis, disturbing reproductive development, reducing grain filling and inducing premature leaf senescence (Munné-Bosch and Alegre, 2004; Abebe et al., 2010; de Oliveira et al., 2013). Due to drought being an environmental stress, it rarely occurs in isolation, but occurs in combination with other abiotic stresses or factors, like high temperature and a low relative humidity, which increases its severity on the crop development (Zandalinas et al., 2017).

1.5.1 The effects of drought on wheat production and productivity

Wheat is a very susceptible crop when exposed to drought. All growth stages of wheat are highly prone to drought stress. Early season drought affects wheat development by reducing germination and vigor, which are necessary for good crop establishment (Bayoumi et al., 2008). Dhanda et al. (2004) reported of more than 50% reduction in percentage germination, root and shoot length on wheat seedlings subjected to osmotic stress. Drought stress also delays the emergence of wheat seedlings and reduces the length of the coleoptile (Rauf et al., 2007). As a result, seedling establishment and growth is reduced, and development of a good root system is compromised (Blum, 1996). In a study by Guedira et al. (1997), it was observed that seminal roots that developed two days after germination were extremely sensitive to dehydration and did not resume their growth when sufficient water was made available and although new roots replaced them upon rehydration, the new root system was less developed than the one that was destroyed.

Susceptibility to drought stress increases as seed progresses from germination to seedling stage with seed embryos showing a high resistance to drought stress (Blum et al., 1980; Blum, 1996). Blum et al. (1980) reported that the ability of wheat seedlings to tolerate drought stress is greatly diminished when the first leaf emerges from the coleoptile. As the plant continues to develop, drought stress will reduce the leaf area of a plant, which eventually reduces transpiration (Duan et al., 2017). This reduction in leaf area corresponds to a reduced capacity of the plant to carry out photosynthesis, which negatively affects final grain yield.

Drought occurring from seedling stage to maturity reduces tiller development and increases the death of tillers (Wang et al., 2017). However, if water conditions improve before maturity, yield recovery is observed due to increased number of grains per spike and improved grain weight (Nagarajan and Nagarajan, 2009). The extent of the recovery is largely dependent on the duration of the stress, with longer periods of stress leading to poorer yield recovery (Blum et al., 1990; El Hafid et al., 1998). Sarto et al. (2017), reports that drought stress that occurs at the stem elongation stage reduces the number of spikes produced resulting in lower yields. However, the plant compensates the loss of spikes by transporting all synthesized assimilates to the remaining fertile tillers. When optimum moisture returns at later growth stages after drought stress occurs at the vegetative stage, late tillers can develop which can significantly enhance the final yield of the crop (Mogensen et al., 1985). In a study conducted by Talukder et al. (1987), late tillers contributed 39% of the final yield, thus compensating for the yield loss from undeveloped normal tillers.

1.5.2 Terminal drought stress and its effects on wheat production

Among all forms of drought stress, end of season or terminal drought is most damaging to wheat development and causes variability in wheat yield (de Oliveira et al., 2013). This is because the major developments in reproduction have a direct bearing on the yield that is achieved by the crop. Terminal drought causes loss of yield by reducing the grain filling rate and duration (Ahmadi and Baker, 2001; Nawaz et al., 2013; Ebadi and Eghbali, 2017), the grain weight (Nawaz et al., 2013), the number of grains per spike (Denčić et al., 2000; Nawaz et al., 2013) and increasing pollen sterility (Lonbani and Arzani, 2011; Webster, 2014).

Decrease in chlorophyll content during drought stress has also been observed during terminal drought (Lonbani and Arzani, 2011), which affects the photosynthetic rate of the plant and production of photo-assimilates required during grain filling, resulting in lower yields (Sayar et al., 2008).

When drought stress occurs during flowering, there is a delay or inhibition of flower development (Saini and Westgate, 1999). The number of florets formed, and the resulting seed set is much lower in wheat plants subjected to drought than those under well-watered conditions (Westgate et al., 1996). It was observed by Dorion et al. (1996) that if wheat plants experience water stress during meiosis in pollen mother cells, the grain set can be reduced by 40 to 50%. Reduction in seed sets as high as 89% in some cultivars have been reported (Briggs et al., 1999). The reduction in grain set leads to a lower grain yield per spike, although there may be increases in individual grain weight (Saini and Aspinall, 1981). This reduction in grain set is attributed to an increase in pollen sterility. The reduced viability of mature pollen grains under water stress cannot be reversed upon improved soil water conditions and is thus considered as the major cause of grain loss in wheat under drought (Ji et al., 2010).

The development of the grain from the fusion of the gametes to the growth and development of the endosperm are sensitive to water stress and are critical in achieving good yields in cereals (Barnabás et al., 2008). Saini and Westgate (1999) divided kernel development in wheat into three phases viz. "*Phase 1*" or "*lag phase*" characterized by a rapid gain in kernel fresh weight, "*Phase 2*" is the grain filling period identified by an increase in dry matter accumulation and "*Phase 3*", which is associated with the maturation of the grain. These phases do not have an abrupt end in their cycle but overlap into each other.

The capacity of grain to store assimilates is determined by cell division and cell enlargement, which largely occur during early grain development (Nicolas et al., 1984). According to Gleadow et al. (1982), the final size of the grain is influenced by the rate of increase of the endosperm cell number with more endosperm cells indicating the availability of more sites for starch deposition. Therefore, the occurrence of drought stress during early grain development will negatively affect cell division leading to a lower number of endosperm cells, which translates into a substantial yield reduction (Saini and Westgate, 1999). Furthermore, in a study conducted by Fábián et al. (2011), drought stress limited the expansion of endosperm cells thereby reducing the amount of water available to the developing grain. This led to high yield reduction due to depressed kernel growth and starch accumulation.

Starch, which makes up more than 80% of the endosperm dry weight constitutes the major part of the grains volume and contributes most to the final weight of the grain (Li et al., 2015). The starch is made up of two types of granules; the A-type granules which are larger and lenticular in shape and B-type granules which are smaller and spherical (Brooks et al., 1982). The A-type granules are formed first, a few days after endosperm formation, followed by the formation of the B-type granules a few days later (Bechtel et al., 1990). According to Brooks et al. (1982), the size of the A-type granules and the number of the B-type granules are reduced when wheat is subjected to drought stress after anthesis. Fábián et al. (2011) argued that the reduced number of B-type starch granules signifies that endosperm cell division has stopped leading to the sink capacity of the wheat kernel being reduced. The authors further stated that plants subjected to stress fail to recover the number of B-type granules even after watering and show less B-type granules in mature grain than well-watered plants.

At the end of the lag phase, the sink potential will have been determined and grain filling begins (Saini and Westgate, 1999). Grain filling is the major determinant of the final grain weight (Xie et al., 2015). The major source of carbohydrates that make up the final weight of the grain are from photosynthesis (Evans and Rawson, 1970). The other source of carbohydrates for grain rowth are assimilates stored in the stem or other plant parts before and after anthesis (Kobata et al., 1992). As a result, large grain yield losses that are observed when drought stress coincides with grain filling are mainly caused by reduced starch accumulation leading to a reduction in grain weight (Barnabás et al., 2008).

Grain filling rate and duration are the key components of final yields of cereal crops (Yang and Zhang, 2006). Grain filling duration is the time from heading to physiological maturity (Talbert et al., 2001). Longer grain filling durations are associated with high yields in wheat (Hunt et al., 1991). When compared to rice, it has been noted that wheat is more sensitive to a shorter grain filling duration (Yang and Zhang, 2006). Drought stress has been implied to shorten the grain filling period in wheat, leading to lower yields (Farooq et al., 2014). According to Semenov et al. (2009), drought stress hastens crop maturity before the end of grain filling is reached, thus reducing translocation of assimilates to the grain. Altenbach et al. (2003) also reports that drought reduces the time for starch accumulation in spring wheat. Wardlaw and Willenbrink (2000) further noted that the decline in the kernel size of wheat subjected to drought stress is mainly a result of shortening of the grain filling period.

A high grain filling rate reflects rapid accumulation of dry matter in wheat grains (Xie et al., 2015). Madani et al. (2010) reported that drought stress can lower the grain filling rate and the allocation of dry matter to grain when it occurs after anthesis resulting in a significant loss of grain yield. However, there have been some reports that mild water stress during grain filling increases the rate of grain filling and promotes remobilization of stored assimilates from other plant organs to the grain (Yang and Zhang, 2006). Therefore, if the grain filling period is reduced, compensation of grain yield can be achieved by increasing the grain filling rate

(Duguid and Brule-Babel, 1994). As a result, Bruckner and Frohberg (1987) proposed that obtaining high grain filling rates should be the objective of plant breeding programmes aiming to achieve higher grain yields in areas that experience a shorter growing season due to terminal drought stress in wheat.

1.6 Drought tolerance

To cope with drought stress, plants have developed a variety of mechanisms at morphological, physiological, biochemical, cellular and molecular levels (Nezhadahmadi et al., 2013; Fang and Xiong, 2015). Tolerance to drought in plants can be grouped into four groups namely drought escape, dehydration avoidance, drought tolerance and drought recovery (Fang and Xiong, 2015).

Drought escape is achieved when a plant completes its life cycle early before the effects of terminal drought set in (Franks, 2011). Therefore, most scientists do not consider escape as a form of drought tolerance (Fischer and Maurer, 1978) since the plant does not experience any drought stress. Early maturing varieties which flower early and have a shorter grain filling period have been shown to produce higher yields when late season drought occurs than late maturing varieties in some studies (Fischer and Maurer, 1978; van Ginkel et al., 1998). This better performance is realized by early maturing varieties because they flower earlier and make use of available moisture to achieve better seed set and higher seed mass (Kooyers, 2015). However, earliness is associated with a compromise on the yield potential of a crop due to reduced time for photo-assimilate production and grain filling (Zaharieva et al., 2001).

Dehydration avoidance refers to the plants ability to cope with drought by avoiding dehydration through either increasing water uptake to keep up with rapid water loss or conserving water through reduced water loss (Chirino et al., 2011; Aslam et al., 2015). Increased water uptake can be achieved if a crop has a deep and large root system. However, based on a study by Ehdaie et al. (2012), the positive response of a large root system to drought is only achieved when there is enough soil moisture that can be accessed by the roots during the grain filling period to enhance grain growth and yield. On the other hand, crops conserve water by employing a variety of mechanisms. These include increasing leaf cuticle thickness (Griffiths and Paul, 2017), stomata closure, leaf area reduction (Sarto et al., 2017) and leaf rolling (Farooq et al., 2014) to reduce the rate of water loss through transpiration.

Drought tolerance occurs at the tissue or cellular level by stabilizing and protecting cellular and metabolic function (Tuinstra et al., 1997). According to Griffiths and Paul (2017), this is achieved by the accumulation of osmo-protectants and production of anti-oxidants that aid in cellular protection during periods of water stress to maintain homeostasis. Stay green properties of a variety also has a strong bearing on the level of drought tolerance of a plant (Farooq et al., 2014). Osmo-protectants can be categorized into three groups according to (Szegletes et al., 2000; Singh et al., 2015) that include amino acids (e.g. proline and ectoine), sugars and polyols (e.g. trehalose, sorbitol and mannitol) and ammonium compounds (e.g. glycine betahine and b-alanine betahine). However, the extent to which these osmo-protectants precisely influence the response of plants to drought stress remains unclear (Mwadzingeni et al., 2016a).

1.7 Genetic diversity and analysis for drought tolerance in wheat

Agricultural scientists are faced with the challenge of improving crop production and ensuring food security for a rapidly increasing population in a world that is being increasingly threatened by water scarcity (Assouline et al., 2015; Merchuk-Ovnat et al., 2016). This can be achieved by crop improvement through plant breeding efforts to produce drought tolerant cultivars (Merchuk-Ovnat et al., 2016). There has been a drive to produce drought tolerant cultivars over the last thirty years for semi-arid areas with limited success being achieved (Monneveux et al., 2012). Although some success has been achieved, progress has been very slow, especially relative to the funding and effort put in by plant breeders and researchers from other fields (Mwadzingeni et al., 2016a).

Successful crop improvement relies on the presence of sufficient genetic variability from which selections are made. Higher variability leads to more efficient selection. To choose an appropriate breeding strategy that will lead to improvement of target characters, evaluation of variability among available germplasm is required (Singh et al., 2012). This is necessary because the loss of genetic diversity can hinder progress in breeding of better performing cultivars that are tolerant to abiotic stresses and adapted to different environments (Allen et al., 2017). One of the simple ways used to broaden genetic variation is hybridization of genotypes within a crop species. According to Mwadzingeni et al. (2017), there is still sufficient genetic variability within elite wheat cultivars that can be used for drought tolerance improvement. This is supported by the continued success in achieving genetic gains in plant breeding programs under drought stressed environments (Manes et al., 2012).

1.8 Genetic gains in wheat breeding for drought tolerance

Breeders have sought to increase genetic gains in wheat as they seek to improve performance under drought stress in target environments (Langridge and Reynolds, 2015). Success has been achieved in increasing genetic gains with reports of improved performance in various yield trials. According to Manes et al. (2012), increases of yield around 1% per annum has been observed in low yielding environments affected by drought stress around the world.

Lantican et al. (2001), reported that greater success due to genetic gains showed that the yield increases that have been achieved in marginal environments exceeded those achieved in optimum growth conditions after the Green Revolution period. This success that has been achieved can be attributed to the setup of breeding platforms which allow exchange of genetic resources and provide free information on yield trials by the International Maize and Wheat Improvement Center (CIMMYT) (Reynolds et al., 2015).

1.9 Breeding for drought tolerance in wheat

Drought tolerance is a complex trait which is controlled by many genes located on quantitative trait loci (QTLs). The expression of these genes is influenced by environmental factors and stage of plant development (Kosova et al., 2014). To further add to this complexity of drought tolerance screening, the variability in the occurrence and duration of drought is high (Lopes et al., 2014).

Selection for drought tolerance should produce crops that not only can survive drought, but those that can give optimum yield under drought conditions (Fleury et al., 2010). A drought tolerant genotype should perform significantly better than the average of other genotypes in an environment where yield is limited by water deficit at some stage of crop development (Quarrie et al., 1999). As such, a proper selection strategy should be adopted to achieve better results in breeding for drought tolerance. Richards et al. (2010) argued that the best environment in which to select for drought tolerance is in well-watered conditions as this is more efficient and has been proved to increase yields under drought conditions. However, Tester and Langridge, (2010) highlights the need for selection under stressed conditions to increase yields in low yielding areas. Therefore, selection of genotypes under both stressed and non-stressed environments simultaneously, is likely to be more efficient in identifying genotypes that perform well under drought without a major yield penalty in optimum conditions.

Selection for drought tolerance under stress can be done in the field or in greenhouses. Evaluating for drought tolerance under field conditions remains the most effective way to screen for drought tolerance (Negin and Moshelion, 2017). This is because field conditions represent the natural conditions in which the crop is grown and give a more reliable picture of the performance of the genotypes under production conditions (Hall, 2000). Selection in the field under natural drought conditions is challenging due to the unpredictable nature of drought response, therefore screening can be done in rain out shelters (Farooq et al., 2009) or by use of the rain out systems. However, rainout shelters have the major disadvantage of increasing construction and maintenance costs as well as limiting the area available for carrying out the experiments (Rauf et al., 2016).

In the greenhouse, breeders can use pots to grow crops for drought screening, which gives the advantage of controlling the growing environment. The breeder can manage the different factors that occur in the natural environment to distinguish the causes and effects of the factors more closely (Hall, 2000). Nevertheless, the use of pots in the greenhouse constrains root growth and adequate drainage (Hasanuzzaman et al., 2017). In addition, pots dry out quickly when irrigation is stopped which might not allow the plant to adjust to the new conditions which it might be able to do when there is gradual drying in the field (Negin and Moshelion, 2017). This gives an inaccurate measure of the performance of the tested genotypes in target environment.

1.10 Inheritance of drought tolerance

Virtually all plant traits are influenced to some extent by genetic factors (Hayes et al., 1955). The final appearance and performance of a genotype or its phenotype is a product of the interaction between genetic factors and the environment. The proportion of the phenotype that is attributable to the genetic factors is termed heritability. Thus, the success of conventional plant breeding programs is influenced by the heritability of the traits of interest, which represents the genetic information that can be transferred from the parents to the offspring. An understanding of inheritance is also essential in understanding the extent of genetic variation in a population and the genetic gains that can be achieved after selection (Melo et al., 2017).

Estimation of heritability provides information on the breeding value of a genotype based on its phenotypic characteristics (Mohsin et al., 2009). Heritability helps in predicting the performance of genotypes in subsequent generations, thus enabling a breeder to make more efficient selections (Jamil et al., 2017). Heritability estimates can be grouped into broad sense and narrow sense heritability. Broad sense heritability "*estimates the ratio of total genetic variance, including additive, dominance and epistatic variance to the phenotypic variance*" whereas narrow sense heritability "*estimates the additive portion of the total phenotypic variance*" (Riaz and Chowdhry, 2003).

Genetic advance is the expected response to selection and an indicator of genetic progress that is expected from selection (Ahmed et al., 2006). The most ideal condition for selection is when high heritability occurs in the presence of high genetic advance, which shows the presence of additive genes for that trait, indicating that selection for that trait can lead to successful crop improvement (Ogunniyan and Olakojo, 2014).

Attaining high grain yield is the goal of growing any grain crop and is the most important trait in wheat. Grain yield is a complex trait that is under the control of many genes and is greatly influenced by the environment (Narjesi et al., 2015; Sun et al., 2017). As a result, heritability of yield is low under drought conditions because of high genotype by environment interaction caused by the large and unpredictable variations in rainfall (Farooq et al., 2014). This may hinder the selection for yield under drought conditions, especially in early segregating generations (Riaz and Chowdhry, 2003).

1.11 Early generation selection

The cost of running research activities is high and is often impeded by the lack of enough funds. Different strategies must be employed to reduce the cost of breeding programs and ensure that they are run efficiently and produce progressive output with minimal cost. To achieve this, the breeder must advance segregating populations without losing any promising recombinants that will lead to successful crop improvement (Reddy et al., 2017). Early generation selection is one of the methods that can be used to reduce the cost by only selecting and advancing the best families.

Early generation selection has been employed with success in many crops including cowpea (Sharma et al., 2015) and tef (Abraha et al., 2017). Extension of this success can be introduced into other crops such as wheat. It has been reported that delaying selection until later generations increases the risk of losing better yielding genotypes because the proportion of good recombinants reduces rapidly with advancing generations (Whan et al., 1982; Reddy et al., 2017). Yet, Whan et al. (1982) reported that selection in early and late generations led to similar yield improvement. This signifies the utility of early generation selection as a strategy that can be employed in crop improvement programs without compromising the effectiveness of selection.

Many factors determine the effectiveness of early generation selection in crops. These include, the sensitivity of the trait to the environment, the nature of gene action that is predominant for the trait and the number of genes that influence the expression of the trait (Pinson et al., 2012). Expression of additive gene action is key in ensuring successful selection in early generations as it indicates high heritability and low environmental effect on traits under selection (Kashif and Khaliq, 2003). Reddy et al. (2017) reports good opportunity for selection in F_3 families, by use of higher mean values for all the traits that were under study. However, effectiveness of selection is reduced in early generations when the trait under evaluation is highly affected by the environment (Barman and Borah, 2012).

1.12 Screening of wheat genotypes for yield under drought stress

Screening wheat genotypes for drought tolerance can be done in several ways. According to Rauf et al. (2016), two methods can be used to improve the economic yields of crops under drought stress. These include the empirical approach, in which selection is based on yield or yield components and the analytical approach, which involves indirect selection through morphological, physiological and biochemical traits that are correlated with yield. In addition, genomics and biotechnology are being incorporated in plant breeding programmes to improve drought tolerance in crops (Farooq et al., 2014). Mwadzingeni et al. (2016b) attributes much of the progress in the improvement of wheat performance under drought conditions to the use of morphological traits and yield components. Use of these traits have the advantage of being relatively easy to measure and do not require specialized equipment to collect the relevant data (Pask et al., 2012).

Selection based on yield components and morphological traits is based on the association of those traits with grain yield. Since yield is a complex trait, which is controlled by many genes, direct selection for yield is unreliable and often misleading (Dabi et al., 2016). Therefore, understanding the interrelationship of yield with other yield related traits with simple inheritance helps in choosing which traits to select for, which will indirectly lead to yield improvement (Gelalcha and Hanchinal, 2013). One of the methods that can be used to evaluate the association between yield components and yield is the correlation coefficient analysis (Abinasa et al., 2011).

1.13 Correlation and path analysis

Correlation studies are important in determining the degree of association among different yield contributing traits and their relationship with yield (Akram et al., 2008). It has been observed that under drought stress many traits have a bearing on the final yield produced by the crop (Mehta et al., 2015). Thus, a study on the association of these traits with yield under drought stress conditions is of paramount importance. It provides information that allow the breeder to select for simultaneous improvement of desirable traits leading to better yield performance of the crop (Prasath et al., 2017). Yield components that have been reported to be important in selection for yield under drought in wheat include the number of productive tillers, spikelets per spike, spike length, kernels per spike and thousand grain weight (Mwadzingeni et al., 2016b). Selection for these traits has been seen to be effective in improving the tolerance of wheat to moisture stress (Ahmed et al., 2007).

Many correlation studies have been carried out and have shown association between yield and its components under drought stress. Poor et al. (2015) reported significant correlations of thousand grain weight with grain yield, and spike weight with grain yield. Positive interrelationships have also been reported between spike length, number of spikes, number of grains per spike and thousand grain weight under both well-watered and drought conditions (Eid, 2009). Association among some of these traits suggests that the expression of these traits is under the control of common genes, which can be exploited to aid selection for higher yield under drought conditions (Munir et al., 2007).

Plant height and earliness are among the traits that are targeted for yield improvement in wheat. Drought reduces the overall height in wheat by either reducing the length of the internodes or the number of nodes on the plant (Ahmed et al., 2007). This indicates the negative impact of drought on the physiological processes in wheat leading to reduced height. Days to heading and days to maturity are important traits in identifying genotypes that could escape drought stress (Li et al., 2011; Mwadzingeni et al., 2016b). Plant height and days to maturity have been reported to be positively correlated with yield in moisture stress conditions (Ali et al., 2015; Singh et al., 2017). This is further supported by (Mwadzingeni et al., 2016b) who argued that tall and late maturing genotypes have more time to photosynthesize and accumulate assimilates than shorter genotypes, which translates to better yields. However, plants should not be too tall as this may lead to lodging and substantial yield loss due to partitioning of dry matter to vegetative parts of the plant at the expense of seed yield (Khan et al., 2010).

Other traits important for drought screening include the peduncle length, number of tillers and the harvest index. The peduncle acts as a temporary store of water-soluble carbohydrates during grain filling and its length can be used to select for high yielding genotypes under drought stress (Li et al., 2011). Consequently, the peduncle length is positively associated with final grain yield under both stressed and non-stressed conditions (Rehman et al., 2015). The tillering ability of a plant is also an important contributor to the final yield of the crop. Significant positive correlations of the number of tillers per plant to grain yield have been reported in other studies (Naghavi et al., 2014; Singh et al., 2014). The harvest index is also positively correlated to yield and thus a higher harvesting index translates to a higher grain yield (Bagrei and Bybordi, 2015).

Correlation studies only show the degree of association between traits but does not indicate the magnitude of contribution made by each component to the trait of interest (Khan et al., 2010; Malav et al., 2017). In order to overcome these challenges and be able to interpret the correlations with better clarity, there is need to carry out path analysis (Singh et al., 2012). The path coefficient analysis gives information on the direct and indirect effects of associations between characters and shows the influence of each individual factor and its relative importance in the yield of the crop (Rani et al., 2017). According to Hefny (2011), path coefficient analysis can be used to determine the exact causes and effects of correlations and remove any effects in the correlations that may be misleading. This allows the breeder to identify those traits that are most effectively contributing to yield, which can be used for efficient selection that leads to successful crop improvement (Diyali et al., 2015).

Path coefficient analysis has been carried out for wheat genotypes evaluated under both optimum and drought stressed conditions. Among the morphological traits and yield components that have a direct effect on grain yield under stress conditions, number of tillers, grains per spike and number of spikes per plant have the greatest direct effects (Denčić et al., 2000; Khan et al., 2010; Bagrei and Bybordi, 2015; Naghavi and Khalili, 2017). The number of tillers is directly related to the final yield that is produced by the crop; in other words, more tillers indicate positive association with a better crop stand and higher yields (Jamro and Rashid, 2017). The high number of grains per spike compensates for the loss of yield due to depressed grain weight under drought, leading to better yield (Slafer et al., 2014; Mwadzingeni et al., 2016b). The number of spikes per plant have an influence on the number of grains that are set, which maintains a high yield under anthesis and grain filling stress (Khan et al., 2010).

Spike length is directly related to the number of grains per spike and thus a longer spike results in higher grain number (Thomas et al., 2017). This is important under stress as increased grain number compensates for the yield loss due to poor grain filling under drought stress. Days to maturity also has a direct effect on yield as early maturing genotypes manage to escape severe drought by completing grain filling early (Khan et al., 2010). Stay green is also an important trait that has a direct effect on yield under stress as it prolongs photosynthesis and allows more time for accumulation of photo-assimilates during grain filling (Gelalcha and Hanchinal, 2013).

1.14 Combining ability and gene action

When conducting breeding trials, it is important to identify the best parents possessing desirable traits and understand the mode of gene action that controls the traits for selection. The diallel mating design and its analysis are valuable in estimating genetic parameters as well as the general and specific combining ability of parents and crosses (Salehi et al., 2015). The design allows the breeder to test lines in all possible cross combinations (Khiabani et al., 2015). The general combining ability (GCA) refers to the average performance of a line in different hybrid combinations, whereas specific combining ability (SCA) refers to instances when crosses perform better or poorer than would be expected from the average performance of the lines involved in the cross (Sprague and Tatum, 1942). The presence of high SCA is an indication of non-additive gene action and high GCA signifies the presence of additive gene action and indicates that a character is highly heritable (Kashif and Khaliq, 2003; Fasahat et al., 2016). Information on combining ability can be exploited by plant breeders to develop better performing lines and hybrids by identifying suitable parents for crossing (Machikowa et al., 2011). The identification of good specific combiners is useful in self-pollinating crops to obtain transgressive segregants for some traits in later generations (Kumar et al., 2017).

The major determinant of success in plant breeding programs is the identification of the suitable parents with high combining ability which can be crossed to increase genetic variation and produce high performing progenies for yield and other agronomic traits (Arya et al., 2018). Combining ability of a parental line cannot be solely based upon its superior phenotypic characteristics (Fasahat et al., 2016), because some phenotypically superior lines may produce inferior recombinants and segregating families necessitating the need to carry out combining ability tests to evaluate the performance of the genotypes based on the progenies that they produce (Kumar et al., 2017). Greater genetic distance between parental lines in the presence of additive x additive interaction effects provides the greatest opportunity for better recombinants and superior transgressive segregates for grain yield in wheat (Kumar et al., 2017).

Much of the genetic variability in yield and its components is due to additive gene action although non-additive gene action is of equal importance among yield components (Kashif and Khaliq, 2003). According to Joshi et al. (2004), both additive and non-additive gene action were important in the inheritance of yield and its components but there was predominance of additive gene action as signified by a greater ratio of GCA to SCA (Subhani and Chowdhry, 2000; Kumar et al., 2017). This predominance of additive gene action is important for successful early generation selection and its absence delays the selection of superior genotypes until later generations (Pagliosa et al., 2017).

1.15 Conclusions

Wheat is one of the major and most important cereal that feed the world. Its production is threatened by changing climatic conditions as well as biotic and abiotic stresses. Among these stresses, drought stress is one of the major abiotic constraints to wheat production in the world. It affects the physiological processes of plants leading to heavy penalties on yield and food availability. Breeding for drought tolerance has been identified as the most sustainable way to combat the variable climatic patterns and the declining water levels. Among the breeding methods that can be implemented with reduced cost of variety development, early generation selection provides an opportunity to increase genetic gains under drought. Use of variance components, combining ability estimates and association studies can greatly increase the efficiency of early generation selection in wheat for improved yield. Therefore, future breeding efforts for wheat improvement should use early generation selection as a strategy to improve performance under drought and other stresses.

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CHAPTER 2

Early Generation Selection of Wheat Genotypes for Drought Tolerance and Agronomic Traits

Abstract

Early generation selection can be used to efficiently identify and advance better performing families in plant breeding programs. This study aimed to evaluate F_3 families of wheat and their parents for drought tolerance and agronomic traits and to select the best performing families for genetic advancement. Seventy-eight genotypes consisting of 12 parents and their 66 F_3 families were evaluated using a 13 x 6 alpha-lattice design with two replications in two contrasting water regimes under greenhouse and field conditions in the 2017/2018 growing season. The following agronomic traits were assessed: number of 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), fresh biomass (BI) and grain yield (GY). Significant differences ($P<0.05$) were observed for DTH, DTM, PH, TN, KPS and TKW among the genotypes under the two water regimes. Variance components and heritability estimates among agronomic traits and yield showed high values for days to heading and fresh biomass under drought stress. Genetic advance values of 29.73% and 37.61% were observed under drought-stressed and non-stressed conditions, respectively, for fresh biomass. The families LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 were relatively high yielding in both stressed and non-stressed conditions and are recommended for genetic advancement preferably using the single seed descent selection approach. The study has confirmed the effectiveness of early generation selection of wheat for days to heading and fresh biomass for selection.

Key words: *Early generation selection, genotypic coefficient of variation, heritability, phenotypic coefficient of variation, wheat*

2.1 Introduction

Wheat (*Triticum aestivum* L.) is among major cereal crops grown in the world. It is the main source of carbohydrate for 30% of the human population (Consortium, 2014). Wheat has increasingly become a commodity crop in sub-Saharan Africa (SSA) including southern African countries (Ronquest-Ross et al., 2015). In South Africa, wheat is the most important grain crop after maize (Nhemachena and Kirsten, 2017). In the country it is predominantly grown under the dryland production conditions in some parts of the Free State Province, or winter rainfall condition in Western Cape Province. Irrigated wheat is mainly cultivated in the Northern Cape Province (van der Merwe and Cloete, 2018).

South Africa is the largest producer of wheat in southern Africa (South African Department of Agriculture, Forestry and Fisheries, 2017). However, there has been a significant decline in wheat production in the country in the last 20 years (van der Merwe, 2015). The total wheat production in the country has decreased from 3.5 million tonnes produced in 1988 to 1.5 million tonnes in 2017 (South African Department of Agriculture, Forestry and Fisheries, 2018). Further, the national mean productivity of wheat is 3.76 tons/ha compared with the potential yield of the crop that can reach up to 10 ton/ha (Grain SA, 2018). The low productivity of the crop has been greatly attributed to varied constraints such as recurrent drought, heat stress and other biotic stresses (wheat rusts and insect pests) (Dube et al., 2016).

Drought is one of the greatest challenges limiting wheat productivity in South Africa. Wheat is sensitive to drought stress, and the increasing incidences of drought causes significant reduction on both wheat grain yield and quality. Terminal drought stress is most common and usually occurs during critical stages of wheat development (flowering, heading and grain filling stages) (Farooq et al., 2014), thus severely hampering wheat productivity. The dryland wheat production areas are most affected by drought episodes and the lack of soil moisture before planting.

To offset the national deficits of wheat, South Africa imports wheat mainly from Russia, United States of America and Germany among other countries at an average of 2.2 million tonnes per annum (South African Department of Agriculture, Forestry and Fisheries, 2017). Wheat imports can be effectively reduced by adopting high yielding and drought tolerant cultivars suitable to local climatic conditions. Consequently, breeding for drought tolerance has been the main goal of several national and international programmes.

A pre-breeding programme for the establishment of drought tolerant wheat gene pool was initiated in South Africa by Mwadzingeni et al. (2016). For sustainable wheat production and productivity, it is imperative to establish a well characterized drought tolerant wheat genetic pool. This will allow for the selection of genotypes that have better water use efficiency and effective drought adaptation. According to El-Hendawy et al. (2017), the effect of climate change will lead to more drier seasons in the future that further exacerbates the impact of drought. The unpredictability of droughts in the region also limits preparatory measures, except wheat breeders address the challenge by the use of host plant resistance. The El Nino southern oscillation (ENSO) (Nicholson, 2001), has strong influence and interactions with the inter-tropical convergence zone (ITCZ) causing more drought episodes south of the equator (Shiferaw et al., 2014) and has further complicated food security issues in the region. The ENSO has been reported to be the dominant mode of inter-annual variability in tropical climate and has had a greater impact on both the global and regional weather and climate anomalies (Chen and Tam, 2010). Previously, the ENSO effects had a characteristic pattern of causing drought events in cycles of 2 to 7 years south of the equator (Singh et al., 2011). This has led to more common challenges in SSA.

Breeding for improved yield under drought conditions is challenging due to high variability in the timing and amount of rainfall that is received in the testing environment (Farooq et al., 2014; Anvari et al., 2017). There is also need to evaluate a large number of genotypes in order to identify those that perform well under drought stress, which increases the costs of drought screening. Early generation selection can be used to increase the efficiency of advancing breeding populations and reducing the cost required to screen large numbers of genotypes in succeeding generations (Abraha et al., 2017). This is achieved by fixing desirable traits and their combinations in early generations (Singh et al., 2017). Selection is done at the F_2 – F_3 generations to eliminate inferior lines and the most promising lines are then advanced for further analysis (Bettge et al., 2002). This is often essential as resources and funds are often limiting factors in many research activities. However, one of the impediments to early generation selection is the lack of sufficient seed to grow genotypes in large plots (Fischer and Rebetzke, 2018). Therefore, in the presence of adequate numbers of seed, breeders can screen at earlier generations and only carry forward promising lines for future selections.

Yield is a complex polygenic trait which is greatly influenced by the genotype, and environment and their interaction thus selection based on yield alone is often misleading especially under drought stress (Ali et al., 2017). Morphological traits and yield components can be used to aid and improve selection efficiency at early generations. Heritability estimates of economic traits under stress and non-stress environments helps on selecting the best traits for wheat improvement. High heritability estimates under stress means that the trait in question can be selected for improvement under that particular stress. Likewise, lower heritability estimates lower selection efficiency and genetic advance in plant breeding programs (Singh, 2005). The use of heritability estimates, genetic advance and both phenotypic and genotypic coefficients of variability has shown to improve selection efficiency in plant breeding programs (Sohail et al., 2018). The presence of high heritability and genetic advance indicates the presence of additive gene action making selection through these traits more effective (Kumar et al., 2018). Therefore, the objective of this study was to undertake early generation selection of wheat genotypes for drought tolerance and agronomic traits for genetic advancement.

2.2 Materials and methods

2.2.1 Plant materials

Twelve parental bread wheat genotypes obtained from the SA pre-breeding genetic pool were used to generate 66 hybrids, using a half diallel mating design. The parental genotypes were initially obtained from the International Maize and Wheat Improvement Centre (CIMMYT) and were selected and advanced due to their breeding value under diverse drought stress and optimal conditions (Mwadzingeni et al., 2016). Table 2.1 provides the details of the parents used to generate the crosses and their drought tolerance index according to Mwadzingeni et al. (2016).

Table 2.1 List of wheat parents used for the half diallel analysis.

Parent	Name	Pedigree	Drought tolerance index
1	LM02	JIANG 4/4/DUCULA	0.76
2	LM04	ONIX/4/MILAN/KAUZ//PRINIA/3/BAV92	0.86
3	LM05	ACHTAR/4/MILAN/KAUZ//PRINIA/3/BAV92	0.89
4	LM09	SOKOLL*2/ROLF07	0.84
5	LM13	SOKOLL/ROLF07	0.55
6	LM17	ESDA/KKTS	0.75
7	LM21	PRL/2*PASTOR	0.82
8	LM22	MUNAL #1	0.92
9	LM23	QUAIU	1.07
10	LM29	PRL/2*PASTOR*2//SKAUZ/BAV92	0.98
11	LM45	ROLF07/YANAC//TACUPETO F2001/BRAMBLING	0.81
12	LM85	SW94.60002/4/KAUZ*2//DOVE/BUC/3/KAUZ/5/SW91-12331	0.91

2.2.2 Study sites

The study was conducted under field and greenhouse conditions, which are briefly described below.

2.2.2.1 Field experiment

The field experiment was carried out at Ukulinga Research Farm (29^{o} 40′ S, 30^{o} 24′ E; 806 m above sea level) during the 2017/2018 cropping season. Test genotypes (12 parents and 66 F_3 families) were field planted using a 13 × 6 alpha lattice design, with two replications. The spacing between plants was 15cm and the inter-row spacing was 30cm. Five seeds were planted at each planting station and later thinned out to leave three plants per station. Each genotype was planted at nine planting stations giving a total number of 27 plants per treatment for each genotype. The experiments were conducted under two water regimes namely drought-stressed and well-watered (non-stressed) conditions. Drought stress treatment was imposed by withholding water to 35% of field capacity at heading, growth stage 59 according to Zadoks et al. (1974). The field capacity of the soil was measured using a tensiometer. In the non-stressed treatment (control), the plants were well watered throughout the growing period up to maturity. To reduce the impact of untimely rainfall on the experiment, the soil was covered with a custom-made plastic mulch rain out system which inhibited infiltration of rain water in the experimental area.

All other standard agronomic practices for wheat production were kept uniform on both regimes during the experiment. The weather conditions prevalent during the time of the experiment were recorded (Table 2.2). Weather data was recorded on day and night temperatures, precipitation, minimum and maximum relative humidity and daily evapo-transpiration rates.

Table 2.2 Monthly weather data during the field trial at Ukulinga, Pietermaritzburg (2017/2018)

Year	Month	Tmax (°C)	Tmin (°C)	RHmax (%)	RHmin (%)	Rs (MJ/m2)	Rain (mm)	ET (mm)
2017	December	24	15	99	59	17.3	97	105
2018	January	28	16.7	99	53	20	63	126
2018	February	28	17.2	100	55	18.5	88	106
2018	March	26	16.3	100	58	16	164	98

Tmax = average maximum temperature, Tmin = average minimum temperature, RHmax = average maximum relative humidity, RHmin = average minimum relative humidity, Rs = average total radiation, ET = average total evapotranspiration

2.2.2.2 Greenhouse experiment

The greenhouse experiment was carried out in a greenhouse located at the University of KwaZulu-Natal (29º 37′ S, 30º 24′ E). The greenhouse environment had a day and night temperatures of 25ºC and 15ºC, respectively. The humidity was maintained at between 45% and 55% for day and night, respectively. Plants were grown in pots filled with composited pine bark growing media. The pots were arranged in a 13 × 6 alpha lattice design, with two replications. The experiments were carried out under two water regimes namely drought-stressed and well-watered (non-stressed) conditions. Seven plants for each genotype were grown in a single pot and thinned to five plants to ensure an even stand of plants in all pots. Water application was the same for both treatments up to the heading stage of growth. After that, drought was imposed on the stressed treatment by withholding water up to plant maturity. To avoid total crop failure in the stressed treatment, extreme stress was detected by crop visualization followed by watering. In the non-stressed treatment, normal watering continued up to maturity. Control of weeds was done manually, and pests and diseases were controlled using chemicals Chess (active ingredient: pyridine azomethine) and Tilt (triazole); and a bio-control fungus *Ampelomyces quisqualis*.

2.2.3 Data collection

The following agronomic data were collected: 1) days to heading (DTH) measured as the number of days until 50% of the plants had fully emerged spikes, 2) days to maturity (DTM) measured as the number of days until 50% of the plants had reached senescence, 3) productive tiller number (TN) measured as the number of tillers that had managed to set seed, 4) plant height (PH) measured as the height from base of the plant to the point where the spike emerged, 5) spike length (SL) measured from the base of the spike to the tip of the spike, 6) spikelets per spike (SPS) measured by counting the number of spikelets per spike, 7) kernels per spike (KPS) measured by counting the number of kernels per spike, 8) thousand kernel weight (TKW) measured by randomly sampling 1000 kernels and weighing them and 9) fresh biomass (BI) and 10) grain yield (GY) measured after harvesting using an electronic balance at 12.5% moisture content.

2.2.4 Data analysis

A combined analysis of variance (ANOVA) was performed using Genstat (18th edition) (VSN International, 2015) on data for all measured traits. Comparisons of means was done using Fishers least significant difference at 5% level of significance. Variance components were calculated using the same program. Heritability in the broad sense was estimated using the formulae given below (Abraha et al., 2017):

$$\mathbf{H^2 = \sigma^2_g / \sigma^2_p}$$

Where, H^2 is heritability in the broad sense

$\boldsymbol{\sigma^2_p}$ is the phenotypic variance for a particular trait = $\boldsymbol{\sigma^2_p = \sigma^2_g + \sigma^2_{gs}/s + \sigma^2_e/sr}$

$\boldsymbol{\sigma^2_g}$ is the genotypic variance for a particular trait

The phenotypic coefficient of variance (PCV) and genotypic coefficient of variance (GCV) components were computed as follows (Burton and Devane, 1953):

$$\mathbf{PCV = (\sigma_p/\bar{x}) \times 100}$$

$$\mathbf{GCV = (\sigma_g/\bar{x}) \times 100}$$

Where:

$\boldsymbol{\sigma_p}$ is phenotypic standard deviation

$\boldsymbol{\sigma_g}$ is the genotypic standard deviation

$\bar{x}$ is the mean performance for a particular trait

Genetic advance (GA) and the genetic advance as percent of mean (GAM) were calculated using the following formulae (Johnson et al., 1955):

$$\mathbf{GA = k\ H^2\ \sigma_p}$$

Where:

GA = Genetic advance

k is the coefficient of selection intensity

H^2 is heritability in the broad sense for that specific trait

σ_p is the phenotypic standard deviation of that specific trait

Finally, genetic advance as percentage of mean (GAM) was computed as follows (Abraha et al., 2017):

GAM = (GA / $\bar{x}$) × 100

2.3 Results

2.3.1 Analysis of variance

A combined analysis of variance showing degrees of freedom, mean square values and significant tests is presented in Table 2.3. Highly significant differences ($P < 0.01$) were observed among genotypes for DTH, DTM, PH, SL, KPS AND TKW. Significant differences were also observed for TN ($P < 0.05$). The mean squares for site and water regime were highly significant ($P < 0.01$) for all traits except for SPS for water regime. Significant genotype by environment interaction ($P < 0.05$) was observed for PH only. There was no genotype x water regime interaction for all the studied traits. The interaction of water regime and environment was highly significant for most traits except PH, SL and SPS.

Table 2.3 Mean squares and significant tests from combined analysis of variance involving ten phenotypic traits of 78 wheat genotypes evaluated in two sites, under two water regimes and two replications.

Source of variation	df	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	BI	GY
Block	40	13.44***	22.24*	23.87	1.34	128.14**	25.66	20.22	4.61	21361.00	6566.00
Replication	4	3.39	5.963	8.12	24.05***	575.33***	5.18	1.37	41.42	664793.00***	189193.00***
Genotype	77	25.18***	19.69***	45.11***	1.13*	151.52***	21.65	32.39***	27.99**	34020.00	8991.00
Site	1	73.39***	9424.08***	145.39**	2043.78***	15051.71***	1244.17***	4250.21***	736.66***	30683941.00***	4101033.00***
Water Regime (WR)	2	176.64***	3091.86***	261.05***	135.80***	672.66***	69.73	1674.48***	17107.67***	14272314.00***	4520338.00***
Genotype x Site	77	3.05	9.74	22.42*	1.02	34.07	21.12	14.97	22.50	27092.00	7587.00
Genotype x WR	77	1.99	5.83	18.14	0.76	33.72	20.64	13.98	14.81	29268.00	8742.00
Site x WR	1	29.64***	346.51***	5.21	6.26**	4.02	116.46	545.46***	5548.27***	6977520.00***	2237842.00***
Genotype x Site x WR	77	2.06	8.84	20.30	0.93	29.21	23.36	14.01	18.41	24923.00	7145.00
Residual	111	2.33	7.49	15.71	0.84	32.02	22.70	15.77	17.32	26462.00	8126.00
Total	467	5.70	30.643	21.68	4.45	73.71	24.39	28.04	56.83	111848.00	25791.00

* P < 0.05; ** P< 0.01; *** P < 0.001; df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = tillering number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield

2.3.2 Yield and agronomic performance

The overall mean for grain yield observed for all the genotypes was 143.62 g/m^2 and 317.22 g/m^2 under drought-stressed and non-stressed conditions, respectively (Table 2.4). Yield reduction of 54.73% was observed because of drought stress. The highest yielding families under stress were LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 with mean yields of 199.80 g/m^2, 185.20 g/m^2, 179.30 g/m^2 and 175.60 g/m^2 respectively. As expected, performance of genotypes was better in non-stressed conditions than in stressed conditions for all the measured traits, except DTH (Table 2.4). The DTH were similar in both drought-stressed and non-stressed conditions. The least DTM were observed for crosses LM17 x LM85, LM45 x LM85, LM17 x LM29, LM04 x LM45 and LM09 x LM21. Drought stress reduced the average PH, TN, SL, SPS and KPS. Decreased TKW and BI were recorded with 26.84% and 43.12%, in that order, due to the effects of drought stress.

Table 2.4 Mean values of the ten best genotypes and five bottom genotypes for ten quantitative traits of 12 parents and their 66 F_3 families

	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
Entry	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
top ten genotypes																				
LM02 x LM05	50.00	49.75	86.00	80.75	66.17	62.82	4.08	3.63	73.10	67.68	13.11	12.69	34.02	25.12	40.06	30.12	799.70	469.80	395.00	199.80
LM13 x LM45	49.00	50.00	85.50	81.00	65.37	65.10	5.10	3.85	85.00	81.78	14.86	13.60	25.22	21.70	43.13	30.73	863.10	468.90	420.00	185.20
LM02 x LM23	51.00	51.25	85.75	81.50	68.35	65.65	5.13	3.50	82.75	73.95	13.77	11.93	25.35	23.09	45.08	30.55	832.50	463.20	458.00	179.30
LM09 x LM45	49.00	50.75	84.00	81.50	62.60	63.05	4.13	3.73	72.00	69.99	13.21	12.70	22.38	22.21	39.97	31.99	561.30	439.30	237.00	175.60
LM13	51.25	52.50	85.00	82.75	62.60	66.00	4.35	4.08	70.70	75.75	13.37	14.20	26.10	25.59	36.48	26.21	736.30	463.30	350.30	175.50
LM13 x LM85	47.75	50.50	84.00	81.00	63.82	61.97	4.65	4.15	69.60	71.53	12.96	13.64	24.94	22.66	40.02	29.44	712.20	481.30	324.10	173.20
LM02 x LM21	48.00	49.00	85.75	80.50	56.90	59.65	3.50	3.58	67.60	74.80	11.20	12.70	23.15	24.48	37.48	31.45	525.60	422.70	229.00	172.90
LM04 x LM21	49.50	49.25	84.75	80.75	58.12	60.90	3.95	3.73	78.10	74.99	14.45	13.50	27.72	19.26	41.01	38.49	637.40	425.30	304.60	169.30
LM22 x LM23	47.25	50.25	85.50	81.75	64.62	64.60	4.08	3.53	75.00	71.27	13.61	13.00	28.66	24.44	39.40	30.09	750.40	436.50	313.80	167.70
LM02 x LM17	49.00	49.50	86.00	80.50	62.37	65.05	4.65	3.98	72.85	69.75	12.26	12.64	23.80	27.38	39.41	29.30	635.30	406.00	287.20	166.80
bottom five genotypes																				
LM05 x LM85	48.50	49.75	84.25	79.75	60.42	60.45	4.18	3.00	68.55	65.04	41.12	12.60	23.61	21.01	39.22	26.55	589.30	333.80	244.60	113.80
LM85	51.75	51.25	85.25	78.25	61.02	62.45	4.30	2.80	73.55	72.14	13.87	13.25	26.44	23.55	37.55	23.80	660.20	382.00	295.40	113.00
LM17 x LM85	46.75	48.00	82.00	76.50	61.67	58.20	4.83	3.63	73.70	69.57	12.35	12.04	23.64	21.40	40.18	23.82	750.30	312.70	382.90	110.60
LM05 x LM17	48.75	50.00	84.00	80.50	64.02	55.72	3.95	3.14	73.60	70.44	13.23	12.25	26.90	20.15	37.85	30.54	631.00	379.10	284.00	101.10
LM05 x LM22	56.00	57.25	92.00	84.50	66.02	59.47	5.20	2.50	72.55	67.41	14.06	13.09	27.21	18.21	36.85	29.54	1088.40	342.30	460.00	90.00
Mean	49.56	50.63	84.92	80.47	62.38	61.09	4.51	3.57	74.00	71.88	13.54	12.83	25.21	22.22	39.31	28.76	701.47	399.00	317.22	143.62
CV (%)	2.52	3.01	3.27	2.88	6.58	5.73	21.81	22.90	7.53	7.19	48.42	8.41	16.53	16.54	8.59	14.34	29.11	20.10	35.89	25.18
SED	0.88	1.08	1.96	1.64	2.90	2.48	0.70	0.58	3.94	3.65	4.63	0.76	2.96	2.58	2.38	2.92	144.40	56.72	80.13	25.62
LSD (5%)	1.75	2.13	3.88	3.24	5.74	4.90	13.75	1.15	7.79	7.23	9.16	1.51	5.85	5.11	4.72	5.77	285.60	112.20	158.50	50.68

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stress, DS = drought-stressed

2.3.3 Variance components, heritability estimates and genetic advance

GCV, PCV, H^2, GA and GAM for both stressed and non-stressed conditions are presented in Tables 2.5 and 2.6. PCV values were higher than GCV values for all the traits for both water regimes. Under non-stressed conditions, the highest GCV values were observed for GY (8.11%), BI (7.26%) and KPS (6.93). The highest GCV values in drought-stressed conditions were for TN (6.56), GY (6.43) and KPS (5.43).

The heritability among the traits varied in both water-stressed and non-stressed conditions (Tables 2.5 and 2.6). Heritability estimates were generally higher in non-stressed condition than drought-stressed conditions for all traits except fresh biomass and grain yield. High heritability was observed in stressed conditions for BI (93.53%) and DTH (78.81%). Under non-stressed conditions only DTH showed high heritability (84.11%). Spike length with values of 67.31% and 60.98% had moderate heritability under both water regimes, respectively. Low heritability ($H^2 < 50\%$) was observed for DTM, PH, TN, SL, SPS, KPS, TKW and GY under both water regimes. The heritability of GY were 17.64% and 14.42%, KPS were 28.47% and 41.28% and PH were 32.62% and 34.46% under drought-stressed and non-stressed conditions, in that order. BI had low heritability value of 17.59% in non-stressed conditions.

The expected genetic advance (GA) varied widely under drought-stressed and non-stressed conditions for the measured traits (Tables 2.5 and 2.6). Higher genetic advances of 29.73 g/m^2 and 6.84 g/m^2 were recorded for BI and GY under drought stressed conditions, in that order. However, the genetic advances of the two traits were 37.61 g/m^2 and 17.12 g/m^2 under non-stressed conditions, in that order. Other traits including DTH, DTM, PH, TN, SPS, KPS and TKW showed relatively low values of expected GA varying from 0 tillers for TN to 2.56 days for DTH under both water regimes, except for spike length which had a GA of 5.01 mm and 6.09 mm under drought-stressed and non-stressed conditions, respectively. The GAM was the highest for BI (7.45%), SI (6.97%) and KPS (5.10%) under drought-stressed condition. The GAM for spike length was 8.23%, kernels per spike (7.84%), days to heading (5,65%) and GY (5.42%) under non-stressed condition. All the other traits such as DTM, PH, SPS and TKW show moderate to low GAM.

Table 2.5 Genetic parameters for morphological characters and yield components in 78 wheat genotypes under drought stressed conditions.

Trait	GCV (%)	PCV (%)	H^2 (%)	GA (%)	GAM (%)
DTH	3.23	3.64	78.81	2.56	5.05
DTM	0.96	2.13	20.17	0.61	0.76
PH	2.56	4.48	32.62	1.57	2.57
TN	6.56	14.21	21.32	0.19	5.33
SL	5.07	6.49	60.98	5.01	6.97
SPS	2.22	4.96	19.96	0.22	1.74
KPS	5.43	10.18	28.47	1.13	5.10
TKW	0.00	8.74	0.00	0.00	0.00
BI	4.38	4.53	93.53	29.73	7.45
GY	6.43	15.31	17.64	6.84	4.75

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = tillering number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield, GCV = genetic coefficient of variation, PCV = phenotypic coefficient of variation, H^2 = Heritability, GA = genetic advance, GAM = genetic advance as a percentage of the mean

Table 2.6 Genetic parameters for morphological characters and yield components in 78 wheat genotypes under non-stressed conditions.

Trait	GCV (%)	PCV (%)	H^2 (%)	GA (%)	GAM (%)
DTH	3.50	3.82	84.11	2.80	5.65
DTM	1.25	2.31	29.44	1.02	1.20
PH	2.76	4.70	34.46	1.78	2.85
TN	0.00	12.66	0.00	0.00	0.00
SL	5.70	6.95	67.31	6.09	8.23
SPS	0.00	24.46	0.00	0.00	0.00
KPS	6.93	10.79	41.28	1.98	7.84
TKW	3.73	6.27	35.27	1.53	3.89
BI	7.26	17.32	17.59	37.61	5.36
GY	8.11	21.36	14.42	17.12	5.42

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = tillering number, SL = spike length, SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight, BI = fresh biomass, GY = grain yield, GCV = genetic coefficient of variation, PCV = phenotypic coefficient of variation, H^2 = Heritability, GA = genetic advance, GA = genetic advance as a percentage of the mean

2.4 Discussion

The high significance values among the wheat genotypes for DTH, DTM, PH, SL, TN, TKW and KPS (Table 2.3) indicates that the tested families showed abundant genetic variation for effective selection for drought tolerance using agronomic traits. Similar results of high genotype differences for these traits have been reported in different moisture regimes in wheat (Eid, 2009; Mwadzingeni et al., 2017).

The significant differences observed among the wheat genotypes when tested under drought-stressed condition, except for spikelets per spike, indicate the negative influence of moisture stress on the expression of the assessed traits (Table 2.3). This led to reduced performance of the genotypes for these traits due to impaired physiological performance as pinpointed by Farooq et al. (2014) who stated that drought affects wheat physiology by reducing metabolic functions, reducing stomatal conductance, causing tissue dehydration and increasing leaf senescence. Reduced performance due to drought stress in yield components has also been reported in other studies (Saleem, 2003; Allahverdiyev et al., 2015). The genotype by water regime interaction was non-significant for all traits indicating that the genotypes kept their rankings in the different water regimes.

The presence of high CV (Table 2.4) for some traits such as GY and BI was expected and thus selection based on yield alone is not dependable. The high CVs also show the variability that is associated with drought trials making them harder to repeat than other agronomic trials (Rehman et al., 2015). Low CVs were recorded for DTH, PH and SL showing that these traits could be used with more reliability for evaluating wheat genotypes.

Higher PCV values than the GCV values (Tables 2.5 and 2.6) were observed for the tested traits indicating the effect of environment on the phenotypic expression of the traits (Ali et al., 2008)**.** However, the GCV and PCV values for DTH and BI (Table 2.5) were similar under drought-stressed condition indicating that most of the variation for these traits would be attributable to genetic effect (Khan and Naqvi, 2011). This provides a great opportunity for efficient selection using these traits because their expression is controlled to a large degree by the genetic variation of the genotypes. DTH is an important trait for selection for drought tolerance. This trait is a means of drought escape ensuring higher yields under terminal drought stress. This provides a great opportunity to select genotypes for early heading and maturity, and high yield potential in drought stress conditions (Abraha et al., 2017).

High heritability for a trait shows that the phenotypic expression of the genotype is a good indicator of the genetic potential of the genotype. BI showed low heritability under non-stressed condition, but high under drought-stressed condition (Tables 2.5 and 2.6). Similar results have been reported by Ahmadizadeh et al. (2011). Low heritability observed for DTM, PH, KPS and TKW under both stressed and non-stressed conditions (Tables 2.5 and 2.6) indicate a large impact of the water regime and the sites on the expression of these traits. The heritability for these traits was much lower in the drought-stressed conditions than non-stressed conditions suggesting the impact of drought-stress on reducing heritability of key traits. The decrease in heritability values under drought-stressed condition signifies the difficulty in selection of genotypes for drought tolerance under stress necessitating testing of genotypes in both well-watered and drought-stressed conditions. Similar result showing reduced heritability values under drought stress were reported by (Eid, 2009; Dorostkar et al. 2015; Shukla et al. 2015). Therefore, based on the observed heritability, selection using DTM, PH, TN, KPS and TKW may not lead to any genetic gain being realised.

High heritability alone is not sufficient in predicting the breeding value of a genotype but denotes the amount of genetic variation that is expressed in the phenotype. Genetic advance serves to estimate the expected response to selection for a certain trait. Therefore, occurrence of high heritability and high genetic advance signify the presence of additive gene action for the trait and thus selection for that trait will lead to genetic gain for that trait (Jatoi et al., 2012). Under such conditions, employing early generation selection is advisable as selection at this stage will be effective in identifying superior families. High heritability was recorded for DTH under both water regimes with high levels of genetic advance (Tables 2.5 and 2.6). The similarities in both water regimes was expected as drought stress was imposed at heading stage and therefore there was no impact of stress on the genotypes to this trait. DTH and DTM can be exploited to produce early maturing genotypes that escape drought stress by initiating the reproductive phases of growth when the impact of terminal drought has not set in. The genotypes that showed the least number of days to heading and could be selected for drought escape are LM04 x LM45, LM17 x LM85, LM17 x LM23, LM22 x LM85, LM17 x LM22 and LM09 x LM17.

Fresh biomass had the highest genetic advance under both drought-stressed and non-stressed conditions suggesting great potential for early generation selection. However, only in the stressed condition was the highest genetic advance observed in the presence of high heritability. This suggests that the genetic component for fresh biomass is greatly expressed when the plants experience terminal drought stress. Therefore, selection for increased fresh biomass at early generations can lead to substantial genetic gains if selected for in stressed conditions. High biomass in wheat is associated with greater stem and leaf area. This leads to higher yields as the plant has increased photosynthetic area which increases photo-assimilate accumulation (Taheri et al., 2011). This is in agreement with Blum (2009) who suggested that enhanced biomass production due to effective use of water is the major contribution to improved genotypic performance under drought stress. All the top ten genotypes (Table 2.4) in this trial had higher values than mean values for BI under drought-stress. This is ideal for drought tolerance improvement as reported by del Pozo et al. (2016) that the annual increases in wheat yield that have been achieved since the 1960's have been positively correlated to above ground biomass.

Longer spike length (SL) is a desired trait under stress as it is associated with higher grain number (Ahmed et al., 2016). Moderate heritability observed for SL in both water regimes (Tables 2.5 and 2.6) was accompanied with high genetic advance. Therefore, selection for improved spike length at this stage will not be effective. Therefore, selection will need to be delayed until later generation for it to be effective (Rehman et al., 2015).

Grain yield (GY) showed high genetic advance, but the heritability was low in both water regimes. This low heritability for grain yield suggests that the genetic makeup of the genotypes can be influenced under drought-stressed condition. This is further supported by Ahmad et al. (2017) who reported that a low response to selection coupled with low heritability could be a result of environmental error and not a lack of genetic variation. This explains the influence of the environment on GY and the need to use component traits for indirect selection. The highest yielding families in drought stressed conditions were LM02 x LM05 (199.8 g/m^2), LM13 x LM45 (185.2 g/m^2), LM02 x LM23 (179.3 g/m^2) and LM09 x LM45 (175.6 g/m^2). The top three genotypes performed relatively well in both drought-stressed and non-stressed conditions. This agrees with the findings by Foulkes et al. (2007) and Mwadzingeni et al. (2016) who reported that wheat genotypes possessing high yield potential would perform well relatively under optimum moisture conditions as well as under drought stress. Therefore, early generation selection could be effective as the higher yields obtained in the top genotypes is accompanied by higher than the mean performance for thousand kernel weight and fresh biomass.

2.5 Conclusions

Early generation selection has been a successful plant breeding tool to enhance selection efficiency. Selections are done involving several families which offers challenges in terms of research space, time, labour and financial resources needing early generation selection. Significant differences were observed among genotypes for DTH, DTM, PH, TN, SL, KPS and TKW indicating the presence of significant genetic variability among the selected wheat families across drought-stressed and non-stressed test environments. There were also differential environmental interactions among controlled and field experiments. Drought stress has been confirmed to reduce wheat agronomic and yield performance. There was marked genotypic and phenotypic variation for DTH, DTM, PH, TN, SL, SPS, KPS, TKW, BI and GY High heritability and genetic advance were observed for days to heading and fresh biomass. LM04 x LM45, LM17 x LM85, LM17 x LM23, LM22 x LM85, LM17 x LM22 and LM09 x LM17 had the least number of days to heading and can be selected for drought escape. The top performing families were LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 expressing grain yields of 199.80 g/m^2, 185.20 g/m^2, 179.30 g/m^2 and 175.60 g/m^2 in that order. These families should be advanced to the F_4 generation using single seed descent. The study also confirmed the utility of early generation selection on wheat under drought stressed environments in South Africa, the knowledge of which can be beneficial to other breeders in cereal improvement for climate-related stress breeding.

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Appendix 2.1 Mean values of 66 F_3 families and 12 parental lines for ten quantitative traits under drought stressed and non-stressed conditions

Entry	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
Families																				
LM02XLM04	49.25	50.00	85.25	79.75	60.27	62.72	4.33	3.28	71.30	74.92	12.55	13.50	24.49	21.60	39.45	26.51	579.00	367.00	275.70	122.20
LM02XLM05	50.00	49.75	86.00	80.75	66.17	62.82	4.08	3.63	73.10	67.68	13.11	12.69	34.02	25.12	40.06	30.12	799.70	469.80	395.00	199.80
LM02XLM09	49.00	48.50	83.75	79.50	64.37	58.75	5.68	3.83	79.80	68.00	13.93	11.49	25.53	18.66	38.91	31.28	834.20	353.20	381.60	129.00
LM02XLM13	48.75	48.50	83.00	79.25	66.25	64.52	4.35	3.90	76.55	74.88	13.51	12.90	24.20	21.51	36.67	29.54	614.50	412.40	271.00	154.80
LM02XLM17	49.00	49.50	86.00	80.50	62.37	65.05	4.65	3.98	72.85	69.75	12.26	12.64	23.80	27.38	39.41	29.30	635.30	406.00	287.20	166.80
LM02XLM21	48.00	49.00	85.75	80.50	56.90	59.65	3.50	3.58	67.60	74.80	11.20	12.70	23.15	24.48	37.48	31.45	525.60	422.70	229.00	172.90
LM02XLM22	48.00	48.25	83.50	79.00	58.55	60.52	4.05	3.10	64.65	70.23	11.54	11.70	21.01	19.78	39.52	30.76	527.40	386.10	229.20	154.90
LM02XLM23	51.00	51.25	85.75	81.50	68.35	65.65	5.13	3.50	82.75	73.95	13.77	11.93	25.35	23.09	45.08	30.55	832.50	463.20	458.00	179.30
LM02XLM29	49.50	51.75	87.00	83.75	63.92	58.52	4.15	4.15	72.15	70.86	12.88	12.39	22.99	24.89	41.17	31.49	795.50	333.10	355.90	130.00
LM02XLM45	48.25	50.00	82.50	80.00	62.47	58.80	4.15	3.78	74.85	70.23	12.61	11.80	22.34	24.20	39.33	28.85	627.90	362.60	331.30	144.90
LM02XLM85	50.25	51.25	84.00	79.00	64.05	61.02	4.15	4.23	75.45	73.23	13.20	12.89	23.68	22.38	39.12	27.66	610.90	415.60	291.20	151.90
LM04XLM05	48.00	49.00	87.25	81.25	64.02	61.87	4.40	3.38	74.70	73.98	12.86	13.30	26.50	27.51	39.29	26.67	572.40	347.00	224.60	139.30
LM04XLM09	50.25	50.50	85.50	79.50	62.37	58.75	5.05	3.40	81.40	73.96	13.22	11.99	26.13	25.12	41.75	31.44	773.90	374.00	376.20	140.10
LM04XLM13	48.25	49.25	84.00	82.25	62.07	62.72	4.03	3.18	74.55	77.39	13.11	13.65	25.31	25.16	38.46	31.48	574.20	448.60	255.30	159.80
LM04XLM17	47.25	49.25	84.25	79.50	63.07	61.80	4.55	3.60	75.25	72.12	12.77	12.50	24.62	22.52	42.10	28.40	705.30	373.10	318.00	153.20
LM04XLM21	49.50	49.25	84.75	80.75	58.12	60.90	3.95	3.73	78.10	74.99	14.45	13.50	27.72	19.26	41.01	38.49	637.40	425.30	304.60	169.30
LM04XLM22	48.50	49.25	84.50	80.25	61.25	60.45	3.58	3.88	81.50	75.50	14.16	14.24	26.99	22.56	38.86	28.21	603.70	418.50	276.20	131.80
LM04XLM23	56.25	54.00	89.25	83.75	68.42	58.20	4.45	3.33	90.45	77.97	15.87	12.84	32.05	25.82	35.72	27.11	926.00	391.10	409.40	134.60
LM04XLM29	50.50	52.75	86.25	81.25	60.05	60.45	3.88	3.53	79.95	80.15	13.46	13.70	25.69	24.17	40.63	28.71	731.60	412.40	350.40	141.20
LM04XLM45	47.25	47.50	83.00	78.00	59.15	55.27	3.58	2.78	79.80	78.57	13.77	12.59	26.31	23.77	42.64	32.00	708.40	365.00	393.80	146.70
LM04XLM85	50.25	50.25	86.00	79.25	59.37	61.95	4.00	3.23	79.10	82.29	13.13	13.94	30.96	23.67	42.76	29.74	649.00	442.10	309.60	164.40
LM05XLM09	52.00	50.75	85.75	78.25	64.95	62.65	4.70	3.35	76.40	71.56	14.26	12.85	23.77	22.22	39.77	27.60	797.40	391.30	343.10	122.40
LM05XLM13	50.75	52.00	87.00	82.75	65.10	62.52	5.05	4.45	77.10	68.43	14.37	13.10	27.80	24.11	40.29	30.37	1001.30	401.80	467.00	147.80
LM05XLM17	48.75	50.00	84.00	80.50	64.02	55.72	3.95	3.14	73.60	70.44	13.23	12.25	26.90	20.15	37.85	30.54	631.00	379.10	284.00	101.10
LM05XLM21	48.75	50.00	85.00	80.50	60.80	56.80	4.30	4.28	69.45	63.18	13.51	12.54	23.04	21.26	41.10	27.88	675.40	404.20	294.50	155.80
LM05XLM22	56.00	57.25	92.00	84.50	66.02	59.47	5.20	2.50	72.55	67.41	14.06	13.09	27.21	18.21	36.85	29.54	1088.4	342.30	460.00	90.00
LM05XLM23	52.00	52.75	86.75	82.25	61.87	61.55	5.35	3.83	63.90	64.13	13.51	12.65	27.15	22.38	39.02	29.64	812.10	433.90	372.20	154.70
LM05XLM29	49.25	51.25	86.25	79.75	64.92	59.72	4.13	2.75	69.95	69.73	13.52	13.40	32.79	25.64	33.90	28.78	669.00	347.00	301.70	126.70
LM05XLM45	50.50	52.25	86.25	81.25	59.05	59.42	4.05	3.53	70.20	78.27	13.45	13.64	24.30	23.48	38.21	30.00	566.60	429.00	259.70	163.60
LM05XLM85	48.50	49.75	84.25	79.75	60.42	60.45	4.18	3.00	68.55	65.04	41.12	12.60	23.61	21.01	39.22	26.55	589.30	333.80	244.60	113.80
LM09XLM13	50.00	53.75	85.50	83.25	64.97	61.70	4.65	4.08	73.75	74.13	12.62	12.95	20.99	20.50	40.90	30.39	744.30	416.50	297.70	135.00
LM09XLM17	47.50	48.75	85.25	78.75	60.77	60.75	4.58	3.45	73.20	71.69	13.21	13.10	26.66	20.64	38.95	26.26	712.50	411.00	326.70	139.70
LM09XLM21	48.25	49.25	84.25	78.25	60.52	61.07	4.98	3.53	67.50	69.93	12.75	12.30	25.90	22.84	39.95	30.32	718.80	405.80	328.70	147.10

Appendix 2.1 (continued)

Entry	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
Families																				
LM09XLM22	50.25	51.25	87.00	79.00	68.15	64.35	5.28	3.24	75.50	68.59	13.00	12.30	26.13	19.33	41.88	28.08	847.30	407.20	374.90	125.00
LM09XLM23	50.75	51.25	85.25	78.50	58.10	62.12	4.40	3.73	71.75	70.63	11.91	13.15	23.70	19.85	39.23	28.28	629.30	434.70	277.40	142.20
LM09XLM29	49.00	51.00	85.50	82.50	60.80	61.05	5.05	4.65	72.45	70.82	13.71	12.60	26.23	18.82	40.55	30.99	677.50	414.40	295.80	143.60
LM09XLM45	49.00	50.75	84.00	81.50	62.60	63.05	4.13	3.73	72.00	69.99	13.21	12.70	22.38	22.21	39.97	31.99	561.30	439.30	237.00	175.60
LM09XLM85	51.00	52.50	85.50	82.00	61.27	61.10	4.63	4.30	68.85	71.35	12.86	13.19	20.09	20.69	40.10	29.92	589.20	437.50	167.80	154.10
LM13XLM17	48.50	51.00	85.50	80.75	64.15	60.70	4.85	2.68	69.85	69.98	12.70	13.05	25.74	19.33	37.55	26.69	692.00	383.20	324.70	137.80
LM13XLM21	48.00	49.00	83.50	78.75	61.77	62.45	4.88	4.03	72.30	71.49	13.25	12.79	22.98	22.60	39.17	26.44	637.00	399.80	285.80	164.80
LM13XLM22	49.00	49.00	85.00	81.00	66.35	59.75	4.93	3.38	68.25	66.14	14.61	13.30	24.37	18.25	37.00	27.51	714.30	418.70	335.90	145.60
LM13XLM23	51.00	51.00	84.50	81.75	70.75	67.92	4.58	3.63	83.20	77.52	14.35	13.70	26.73	22.07	41.34	28.26	888.10	481.80	394.40	166.00
LM13XLM29	50.50	52.50	85.25	81.00	64.77	65.60	4.28	3.58	73.47	73.89	13.96	13.90	28.44	23.05	39.98	28.34	771.80	481.20	376.50	166.40
LM13XLM45	49.00	50.00	85.50	81.00	65.37	65.10	5.10	3.85	85.00	81.78	14.86	13.60	25.22	21.70	43.13	30.73	863.10	468.90	420.00	185.20
LM13XLM85	47.75	50.50	84.00	81.00	63.82	61.97	4.65	4.15	69.60	71.53	12.96	13.64	24.94	22.66	40.02	29.44	712.20	481.30	324.10	173.20
LM17XLM21	48.25	49.50	82.50	80.75	60.55	57.17	5.15	3.95	71.90	63.75	12.87	12.07	24.39	19.63	34.85	27.55	640.00	345.30	291.60	126.00
LM17XLM22	47.00	48.75	83.75	79.00	60.17	57.85	4.33	3.30	67.15	65.70	12.85	11.85	24.13	21.90	36.30	27.88	644.50	392.00	288.80	153.30
LM17XLM23	46.75	49.00	82.00	80.50	60.82	52.85	4.38	3.05	68.35	63.54	12.25	11.44	22.12	19.26	37.41	27.01	553.30	311.90	234.20	117.10
LM17XLM29	48.00	49.50	83.00	78.00	63.37	57.02	4.60	2.55	76.35	70.33	13.64	12.65	26.99	23.22	39.34	28.38	751.20	343.40	370.80	119.40
LM17XLM45	48.75	48.50	84.50	78.25	53.25	56.22	4.70	3.73	70.45	75.46	11.37	12.69	18.32	20.52	34.91	29.42	482.80	339.20	242.90	115.40
LM17XLM85	46.75	48.00	82.00	76.50	61.67	58.20	4.83	3.63	73.70	69.57	12.35	12.04	23.64	21.40	40.18	23.82	750.30	312.70	382.90	110.60
LM21XLM22	49.00	51.25	84.25	80.25	59.85	62.62	3.80	3.60	72.90	67.63	12.92	13.40	25.93	20.36	37.16	27.00	566.60	407.40	248.40	127.60
LM21XLM23	50.25	51.00	86.50	81.75	60.35	63.80	4.98	3.78	72.45	68.60	13.05	12.34	22.72	20.87	40.35	29.56	593.20	425.20	239.40	159.20
LM21XLM29	49.25	49.25	84.50	79.75	61.15	62.52	3.80	3.35	73.90	71.69	13.14	13.40	26.27	22.57	38.57	29.14	747.50	444.90	325.10	157.10
LM21XLM45	49.50	51.00	83.75	80.50	59.00	60.12	4.95	3.73	74.07	75.18	12.01	12.85	25.66	22.81	36.01	28.08	688.70	440.00	328.40	162.70
LM21XLM85	48.75	50.00	85.50	81.00	59.05	61.47	3.80	3.53	73.00	68.75	13.01	12.35	23.84	21.57	41.63	30.38	587.70	403.00	248.90	155.00
LM22XLM23	47.25	50.25	85.50	81.75	64.62	64.60	4.08	3.53	75.00	71.27	13.61	13.00	28.66	24.44	39.40	30.09	750.40	436.50	313.80	167.70
LM22XLM29	47.75	49.75	82.00	79.75	61.15	59.32	4.65	4.78	67.50	67.14	12.92	12.30	22.39	18.71	37.70	27.32	724.10	375.10	336.10	122.30
LM22XLM45	48.50	48.75	82.00	79.25	62.10	61.90	4.70	3.50	72.80	76.73	12.56	13.40	22.56	15.98	36.11	29.15	672.30	371.60	277.00	116.70
LM22XLM85	48.25	47.50	83.00	78.75	60.57	57.15	4.95	3.65	71.20	62.58	13.51	12.62	22.42	19.14	38.95	27.15	624.80	302.70	267.60	116.00
LM23XLM29	50.00	51.25	85.25	82.50	63.35	64.12	3.85	3.98	79.40	75.44	12.92	13.00	24.84	19.94	42.88	30.37	725.10	365.10	258.40	135.80
LM23XLM45	49.00	50.25	84.50	80.25	60.90	62.27	6.35	3.90	79.60	80.03	12.92	12.65	29.51	21.31	39.27	29.62	741.80	450.60	359.10	154.70
LM23XLM85	48.75	50.00	82.50	78.50	65.40	60.30	4.60	3.28	73.80	70.47	12.66	12.39	24.47	23.05	38.28	26.42	748.50	389.70	313.90	151.50
LM29XLM45	48.50	50.50	84.50	79.75	61.50	61.12	4.30	3.30	72.20	70.95	12.97	12.85	26.05	23.93	38.64	28.21	538.20	363.00	233.90	123.20
LM29XLM85	48.50	51.00	84.50	82.25	60.82	60.50	4.08	3.15	73.55	66.18	13.92	12.40	25.53	24.51	37.31	29.80	662.40	358.60	329.00	153.70
LM45XLM85	47.75	49.00	84.75	77.75	61.80	58.70	4.10	3.48	74.60	76.90	12.46	12.40	22.62	23.44	40.82	26.24	737.20	386.20	326.30	149.10

Appendix 2.1 (continued)

Entry	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
	NS	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**
Parents																				
LM02	49.00	50.75	86.00	81.75	66.12	65.95	4.40	3.60	72.90	73.06	13.02	12.30	27.76	21.91	42.39	30.47	713.70	370.80	331.20	141.90
LM04	53.25	54.75	86.75	82.25	63.47	63.67	5.05	3.03	87.40	80.13	15.17	13.44	27.84	26.71	44.70	29.54	940.30	442.60	472.80	156.30
LM05	53.75	56.75	91.75	83.75	62.12	62.85	4.65	2.73	72.90	70.98	14.01	14.00	24.48	22.63	40.62	27.58	742.00	392.60	294.90	116.30
LM09	53.25	52.75	84.75	80.25	64.05	60.95	5.38	3.70	73.95	68.95	12.91	12.25	24.77	23.08	36.69	26.31	749.20	406.70	312.00	127.70
LM13	51.25	52.50	85.00	82.75	62.60	66.00	4.35	4.08	70.70	75.75	13.37	14.20	26.10	25.59	36.48	26.21	736.30	463.30	350.30	175.50
LM17	48.00	49.25	83.25	80.50	59.12	59.85	4.40	3.83	70.80	67.67	12.11	12.45	23.96	21.22	37.39	26.93	713.10	342.90	353.80	136.80
LM21	50.00	52.00	86.25	81.75	60.30	59.95	4.43	4.28	68.90	67.26	12.53	12.45	21.97	22.25	43.68	27.45	553.40	436.60	228.60	156.20
LM22	50.00	51.00	82.50	77.50	62.82	61.97	4.70	3.58	70.80	71.24	12.46	12.95	25.86	22.69	30.46	24.98	594.60	424.30	240.30	136.10
LM23	53.25	52.75	86.50	82.75	67.85	64.45	5.00	3.93	81.00	76.98	12.56	12.85	24.51	23.59	44.54	27.78	1033.20	430.30	438.50	144.10
LM29	51.00	51.75	78.50	81.00	62.10	58.35	3.83	3.03	67.60	68.62	12.76	11.54	24.57	25.41	39.63	28.68	764.00	313.70	361.50	115.50
LM45	51.75	53.00	86.25	79.50	59.80	61.20	4.65	3.80	83.70	83.02	12.85	13.74	25.37	19.98	40.97	26.55	730.80	419.70	329.90	124.50
LM85	51.75	51.25	85.25	78.25	61.02	62.45	4.30	2.80	73.55	72.14	13.87	13.25	26.44	23.55	37.55	23.80	660.20	382.00	295.40	113.00
Mean	49.56	50.63	84.92	80.47	62.38	61.09	4.51	3.57	74.00	71.88	13.54	12.83	25.21	22.22	39.31	28.76	701.47	399.00	317.22	143.62
CV (%)	2.52	3.01	3.27	2.88	6.58	5.73	21.81	22.90	7.53	7.19	48.42	8.41	16.53	16.54	8.59	14.34	29.11	20.10	35.89	25.18
SED	0.88	1.08	1.96	1.64	2.90	2.48	0.70	0.58	3.94	3.65	4.63	0.76	2.96	2.58	2.38	2.92	144.4	56.72	80.13	25.62
LSD (5%)	1.75	2.13	3.88	3.24	5.74	4.90	13.75	1.15	7.79	7.23	9.16	1.51	5.85	5.11	4.72	5.77	285.6	112.2	158.50	50.68

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m2), GY = grain yield (g/m2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stress, DS = drought-stressed

CHAPTER 3

Combining Ability Analysis for Yield and Agronomic Traits among F_3 Lines of Wheat under Drought-stressed and Non-stressed Conditions

Abstract

Combining ability analysis is fundamental in plant breeding programs to identify promising parents, and to select and advance high performing families. The objective of this study was to determine the combining ability effects of wheat for yield, agronomic and drought tolerance traits to select best performing parents and F_3 lines under drought-stressed and non-stressed conditions. Sixty-six F_3 families developed from a 12 x 12 half diallel cross along with their 12 parents were evaluated in a 13 x 6 alpha-lattice design under field and greenhouse conditions, with two replications. Data was collected on the number of days to heading (DTH), number of 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), fresh biomass (BI) and grain yield (GY). Significant general combining ability (GCA) effects of parents were observed for DTH, PH and SL under both testing conditions. The specific combining ability (SCA) effects of progenies were only significant for DTH under all testing conditions. The heritability of most traits was low ($0 < h^2 < 0.40$) except for SL which showed moderate heritability of 0.41 under drought-stressed conditions. The GCA/SCA ratio was below one for all the traits indicating the predominance of non-additive gene action. Low negative GCA effects were observed for DTH, DTM and PH on parental line LM17 in a desirable direction for drought tolerance. High positive GCA effects were observed on LM23 for TN and SL, LM04 and LM05 (for SL, SPS and KPS), LM21 (TKW), LM13 and LM23 (BI) and LM02, LM13 and LM23 for GY. Families LM02 x LM05 and LM02 x LM17 were the best performers across the test conditions and are recommended for further genetic advancement.

Keywords: *Combining ability, drought tolerance, gene action, heritability, wheat*

3.1 Introduction

Climate change threatens the global agricultural system to supply enough food to a growing population in a sustainable way (Timmusk et al., 2015). A new and productive approach to agriculture to meet the challenges that are posed by climatic change is necessary if production is to be increased or maintained to meet the growing food demands. Among the major threats of climate change, the increasing unpredictability of rainfall patterns is a major concern to the agricultural sector. According to Zandalinas et al. (2018), the average precipitation expected in subtropical and tropical regions is likely to decrease in the future. Therefore, the direct impact of climate change on crop production and productivity in the form of drought stress is expected to reduce the overall yield of cereal crops globally (Wang et al., 2018).

Drought is associated with limited water availability for crop plants especially during vegetative and reproductive stages leading to reduced yield potential. The most vulnerable areas to drought stress are the semi-arid regions where increased fluctuation of precipitation patterns can have devastating yield loss or complete crop failure (Eigenbrode et al., 2018). These areas represent 70% of the world's arable land (Timmusk et al., 2014). Thus, drought stress is considered to be the most limiting factor to successful crop production in the world (Lonbani and Arzani, 2011).

Dryland wheat production is affected by recurrent drought which is further exacerbated by the compound effect of other biotic and abiotic stresses (Mwadzingeni et al., 2016). Drought stress affects wheat yield in all stages of crop growth, but its greatest impact occurs during anthesis and grain filling (Saradadevi et al., 2017). At anthesis, drought stress is characterised by pollen sterility and reduced number of spikes and spikelets resulting in reduced grain number (Ji et al., 2010). Terminal drought stress leads to rapid leaf senescence and reduced photo-assimilates in the leaves limiting their contribution to final grain yield (Saeidi and Abdoli, 2015). Irrigation can be used to mitigate the effects of drought in some instances. However, irrigation is becoming unsustainable because of the depletion of water reserves and the growing demand for water for other uses (Blignaut et al., 2009), while irrigation facilities are completely absent in some production areas. Therefore, breeding for drought tolerant genotypes that are adapted to local conditions presents the most sustainable way to increase yields in dryland areas.

The success of conventional plant breeding programs is determined by the amount of genetic variation found in the parental genotypes. It is therefore imperative to assess the value of parental genotypes that are used to make crosses. The phenotypic expression of genotypes is affected by the environment. Consequently, it is necessary to estimate the breeding value of genotypes under varying growing conditions (Bazakos et al., 2017). The value of parents can be determined by the performance of their progenies which is referred to as progeny testing or combining ability analysis (Griffing, 1956). Combining ability analysis is fundamental in plant breeding programs to identify promising parents and to select and advance high performing families.

The diallel mating design has been used extensively to estimate combining ability values and identify good combiners in a variety of crops including major crops such as wheat (Farhat and Darwish, 2016), maize (Murtadha et al., 2016), rice (Huang et al., 2015) and minor crops such as mustard (Vaghela et al., 2016) and sesame (Tripathy et al., 2017). The diallel mating design is useful in estimating general combining ability (GCA) and specific combining ability (SCA) effects as well as the mode of gene action controlling key traits (Gholizadeh et al., 2018). It has the added advantage over other mating designs in that it allows the evaluation of parental lines in all possible cross combinations (Patel et al., 2018).

The nature of the gene action that controls the expression of a trait determines the breeding strategy that is implemented to ensure efficient selection. For instance, high general combining ability estimates among parents allows accumulation of additive gene effects through gene recombination and continuous selection (Gautam et al., 2018). High GCA estimates indicate predominance of additive gene action, existence of high heritability and low environmental effect on the phenotype (Fasahat et al., 2016). This presents an ideal condition for effective early generation selection of superior families. On the other hand, high SCA values shows the predominance of non-additive gene action indicating that superior performance cannot be fixed by continuous selection (Patel et al., 2018). Therefore, in self-pollinating crops such as wheat where non-additive gene action is predominant in controlling the expression of key traits, early generation selection will not be successful, and selection will need to be delayed until later generations (Pagliosa et al., 2017).

Combining ability estimates under different growing conditions are necessary given the impact of the environment on phenotypic expression of a trait. Good combining ability estimates under optimum growing conditions will not necessarily lead to better performance under less favourable environments. Reports from different crops suggest that GCA and SCA variances and the nature of gene action varies under different environments and moisture regimes (Gholizadeh et al., 2018; Mwadzingeni et al., 2018). For cultivar release under dryland production systems, combining ability studies should be carried out under both drought-stressed and non-stressed conditions. Therefore, the aim of this study was to determine the combining ability effects and determine the mode of gene action that controls yield and yield components in selected wheat genotypes under drought-stressed and non-stressed conditions.

3.2 Materials and methods

3.2.1 Plant materials

The study used 12 bread wheat parental lines and their 66 F_2 derivatives generated through a half-diallel mating design. The details of parents and crosses were presented in Chapter 2, Section 2.2.1.

3.2.2 Study sites

The study was conducted during the 2017/2018 growing season in two sites which is briefly described below:

3.2.2.1 Field experiment

The field experiment was conducted at Ukulinga Research Farm using a 13 x 6 lattice square design. This was described in Chapter 2, Section 2.2.2.1.

Greenhouse experiment

The trial was conducted using 5L capacity plastic pots as experimental units. The experiments were laid out in a 13 x 6 lattice square design with two replications. This was described in Chapter 2, Section 2.2.2.2.

3.2.3 Data collection

Data was collected on 10 agronomic traits under both the field and greenhouse experiments. Details of the data collected were summarised in Chapter 2 Section 2.2.3.

3.2.4 Data analysis

A combined analysis of variance (ANOVA) was conducted for all the measured traits. This was performed using Genstat 18th edition (VSN International, 2015). Diallel analysis was conducted separately for each of the four test conditions (greenhouse non-stressed, greenhouse drought-stressed, field non-stressed, and field drought-stressed) 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 II, Model I as follows:

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

Where:

μ = population mean

Y_{ij} = phenotypic observation on progenies

g_i = GCA effect of Parent i

g_j = GCA effect of Parent j

S_{ij} = SCA effect of cross between Parent i and Parent j

e_{ijk} = experimental error due to environmental effect

The relative GCA/SCA ratio was calculated for all traits to determine the prevailing gene action using the following formula according to Baker (1978):

GCA/SCA ratio = $2\sigma^2_{gca} / (2\sigma^2_{gca} + \sigma^2_{sca})$

Where:

σ^2_{gca} = variance due to GCA

σ^2_{sca} = variance due to SCA

3.3 Results

3.3.1 Analysis of variance

A combined analysis of variance and mean response of bread wheat genotypes evaluated under drought-stressed and non-stressed conditions was summarised in Table 2.3. The mean squares for combined analysis of variance showed highly significant differences ($P<0.05$) of genotypes for DTH, DTM, PH, TN, SL, SPS, KPS and TKW (Table 2.3). Highly significant ($P<0.05$) differences were observed for water regime by site for all the measured traits except for SPS. The results imply that high variability was present in these genotypes allowing family selection.

3.3.2 Mean performance of genotypes for agronomic traits

Table 3.1 presents the mean performances of families for yield and agronomic traits evaluated across drought-stressed and non-stressed conditions. The results displayed the top 15 and bottom five genotypes based on their yield performance under field and drought-stressed conditions. The mean response of genotypes for DTH was relatively unchanged across all the testing environments. DTM decreased by 3 days and 1.5 days due to drought stress under the field and greenhouse conditions, respectively. Reduction in PH with 0.60 cm and 3.05 cm were recorded under field and greenhouse sites, in that order, due to the impact of drought stress. The top performing families were characterised by a relatively high DTM and PH with low values for DTH. The family LM05 x LM22 which is among the low yielding genotypes had high DTH (57.00 and 57.50 days) and DTM (84.00 and 85.00 days) under drought-stressed conditions in the field and greenhouse testing conditions, respectively. Low yielding families under drought-stressed condition (e.g. LM05 x LM22, LM13 x LM22 and LM17 x LM85) exhibited high yields under non-stressed conditions. Drought stress decreased the mean TN, SL and KPS in both sites. The family LM09 x LM29 maintained high TN under all test conditions. The mean values of KPS decreased by 0.15 and 7.54 due to drought-stress under field and the greenhouse tests, in that order. Under field condition, mean TKW decreased by 17% owing to drought-stress compared with a decrease of 36% under the greenhouse condition. BI decreased by 47% and 53% under drought-stressed and field and greenhouse conditions, respectively. Under field evaluation a mean GY loss of 55% was recoded compared with a loss of 66% under greenhouse condition due to drought stress. The following families were the top yielders under drought stressed condition in the field evaluation: LM22 x LM23 (with grain yield of 189.80 g/m^2), LM04 x LM85 (170.40 g/m^2), LM02 x LM21 (163.00 g/m^2) and LM05 x LM45 (157.60 g/m^2). These families had also high values for SL, TKW and BI. The family LM02 x LM05 consistently performed well providing a mean yield of 154.30 g/m^2 and 245.50 g/m^2 under drought-stressed and (204.50 g/m^2, 578.90 g/m^2) under non-stressed conditions in the field and greenhouse, respectively when compared with all other genotypes.

Table 3.1 Mean performance for 10 agronomic traits of 15 top performing families and five bottom families selected through evaluations of 78 genotypes in two testing sites under drought-stressed and non-stressed conditions.

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Fifteen top families																				
LM02 x LM05	49.50	49.50	50.00	50.50	76.50	80.50	85.00	91.50	64.25	64.25	61.40	68.10	5.25	5.95	2.00	2.20	71.02	77.90	64.40	68.30
LM02 x LM17	48.50	50.00	50.50	48.00	76.50	83.00	84.50	89.00	67.35	63.60	62.75	61.15	6.45	6.40	1.50	2.90	75.92	79.60	63.70	66.10
LM02 x LM21	49.00	48.00	49.00	48.00	77.00	78.50	84.00	93.00	57.25	59.30	62.05	54.50	5.65	4.30	1.50	2.70	78.64	77.60	71.00	57.60
LM04 x LM09	50.50	50.50	50.50	50.00	77.50	80.00	81.50	91.00	62.35	63.55	55.15	61.20	5.60	7.00	1.20	3.10	82.00	87.00	66.00	75.80
LM04 x LM13	50.00	50.00	48.50	46.50	79.50	78.50	85.00	89.50	60.30	65.65	65.15	58.50	4.85	5.75	1.50	2.30	80.61	79.20	74.20	69.90
LM04 x LM85	51.00	51.50	49.50	49.00	78.00	82.50	80.50	89.50	64.95	62.35	58.95	56.40	5.25	6.10	1.20	1.90	90.13	85.10	74.60	73.10
LM05 x LM45	53.50	51.50	51.00	49.50	78.50	82.00	84.00	90.50	60.30	67.30	58.55	50.80	5.55	6.10	1.50	2.00	86.61	80.60	70.00	59.80
LM09 x LM23	51.50	52.50	51.00	49.00	77.50	80.50	79.50	90.00	63.65	59.50	60.60	56.70	5.97	6.00	1.50	2.80	76.61	75.30	64.70	68.20
LM09 x LM29	52.00	49.00	50.00	49.00	79.50	79.00	85.50	92.00	62.00	58.55	60.10	63.05	7.60	7.50	1.70	2.60	74.20	76.40	67.45	68.50
LM09 x LM45	51.00	49.00	50.50	49.00	78.50	78.50	84.50	89.50	63.55	62.95	62.55	62.25	5.25	5.15	2.20	3.10	73.71	78.00	66.30	66.00
LM13 x LM23	51.50	51.00	50.50	51.00	78.50	80.00	85.00	89.00	72.75	67.65	63.10	73.85	5.35	5.25	1.90	3.90	86.11	83.80	69.00	82.60
LM13 x LM85	50.00	47.50	51.00	48.00	77.00	78.00	85.00	90.00	62.35	63.30	61.60	64.35	6.10	6.60	2.20	2.70	79.32	75.50	63.80	63.70
LM21 x LM45	51.50	50.00	50.50	49.00	78.00	81.00	83.00	86.50	57.65	57.80	62.60	60.20	5.45	6.90	2.00	3.00	80.08	79.85	70.30	68.30
LM22 x LM23	49.50	47.00	51.00	47.50	79.00	81.00	84.50	90.00	66.50	64.15	62.70	65.10	5.85	5.25	1.20	2.90	75.81	82.00	66.70	68.00
LM23 x LM45	50.00	51.00	50.50	47.00	78.50	81.00	82.00	88.00	62.65	59.45	61.90	62.35	5.80	9.90	2.00	2.80	85.61	86.40	74.50	72.80
Five bottom families																				
LM05 x LM22	57.00	58.00	57.50	54.00	84.00	91.00	85.00	93.00	61.40	63.00	57.55	69.05	4.10	6.30	0.90	4.10	77.31	73.90	57.60	71.20
LM13 x LM17	51.50	50.00	50.50	47.00	77.00	81.00	84.50	90.50	57.50	65.75	63.90	62.55	3.57	7.50	1.80	2.20	77.81	71.60	62.10	68.10
LM13 x LM22	50.00	50.00	48.00	48.00	77.50	81.50	84.50	88.50	57.00	66.25	62.50	66.45	4.95	6.85	1.80	3.00	69.70	76.10	62.60	60.40
LM17 x LM85	47.50	47.50	48.50	46.00	71.00	77.00	82.00	87.00	58.05	60.60	58.35	62.75	5.95	6.95	1.30	2.70	74.34	76.20	64.90	71.20
LM22 x LM45	47.50	47.50	50.00	49.50	74.50	77.00	84.00	87.00	59.75	61.70	64.05	62.50	5.10	6.60	1.90	2.80	86.90	72.80	66.50	72.80
Mean	49.00	48.50	50.50	47.00	75.50	78.50	84.00	85.50	58.10	58.70	60.55	63.60	7.55	5.90	2.00	3.40	69.10	69.30	65.20	65.70
LSD (5%)	3.14	2.69	2.95	2.29	4.56	6.15	4.68	4.84	7.01	7.08	6.97	9.16	2.16	2.43	0.82	1.34	9.87	10.49	10.73	11.71
SE	1.57	1.35	1.48	1.15	2.29	3.08	2.34	2.43	3.51	3.55	3.49	4.59	1.08	1.22	0.41	0.67	4.94	5.26	5.38	5.87
CV (%)	3.10	2.69	2.93	2.34	2.96	3.84	2.80	2.71	5.69	5.65	5.77	7.41	19.75	19.59	24.55	23.95	6.44	6.65	8.01	8.50

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Table 3.1 continued

Families	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Fifteen top families																				
LM02 x LM05	13.90	14.40	11.50	11.80	26.64	36.06	23.47	32.11	33.24	35.56	26.96	44.45	309.80	401.60	629.90	1198.00	154.30	204.50	245.50	578.90
LM02 x LM17	13.80	14.10	11.50	10.40	32.35	27.48	22.01	20.25	33.54	38.30	25.00	40.50	295.80	368.90	516.30	902.00	145.50	178.60	187.90	393.80
LM02 x LM21	13.50	13.20	11.90	9.20	28.02	28.58	20.72	17.80	34.15	31.83	28.68	43.15	347.90	371.30	497.40	680.00	163.00	168.90	182.60	289.20
LM04 x LM09	13.90	14.90	10.10	11.50	27.02	26.57	23.03	25.82	37.09	37.70	25.81	45.75	331.50	383.10	416.60	1165.00	154.30	188.40	126.10	559.00
LM04 x LM13	14.20	14.50	13.10	11.71	29.78	27.22	20.03	23.46	35.40	31.98	27.59	44.75	332.20	330.90	565.00	818.00	145.60	147.90	174.20	358.40
LM04 x LM85	15.70	14.60	12.20	11.70	26.73	37.26	20.40	24.98	35.24	40.60	24.23	44.90	381.10	449.30	503.10	849.00	170.40	215.20	157.90	402.40
LM05 x LM45	15.60	15.40	11.70	11.50	27.38	27.32	19.33	21.35	34.08	33.38	25.85	43.10	351.30	439.00	506.70	694.00	157.60	185.90	169.50	333.50
LM09 x LM23	14.20	13.00	12.10	10.80	23.69	26.27	15.66	21.27	32.23	33.00	24.33	45.25	345.00	292.50	524.40	966.00	146.90	135.30	137.30	414.30
LM09 x LM29	13.20	14.50	12.00	12.92	23.09	26.43	14.39	26.00	33.51	36.00	28.45	45.05	360.70	329.10	468.00	1026.00	156.30	156.50	130.80	434.10
LM09 x LM45	13.30	14.60	12.10	11.82	24.44	25.72	17.76	19.02	34.40	36.25	29.55	43.65	307.40	347.50	571.20	775.00	150.40	167.80	201.00	306.00
LM13 x LM23	14.50	14.90	12.90	13.80	25.73	27.68	18.02	25.85	32.95	37.59	23.49	45.05	394.10	389.50	569.60	1387.00	156.10	182.80	175.90	602.50
LM13 x LM85	14.69	14.10	12.60	11.81	26.26	23.56	15.43	27.76	30.51	33.15	27.30	46.79	357.80	368.10	604.90	1056.00	155.10	155.90	191.30	492.10
LM21 x LM45	13.80	13.50	11.90	10.50	27.26	26.31	18.05	25.00	29.84	34.85	26.32	37.15	310.90	368.40	569.20	1009.00	144.70	183.00	180.90	471.10
LM22 x LM23	13.90	15.40	12.10	11.80	28.03	32.01	20.62	25.34	34.75	36.93	25.34	41.85	421.50	460.50	451.50	1040.00	189.80	214.00	146.00	413.30
LM23 x LM45	13.90	14.20	11.40	11.60	26.53	32.88	15.64	26.33	32.90	34.15	26.33	44.20	346.40	321.10	554.80	1162.00	149.50	141.20	159.90	568.90
Five bottom families																				
LM05 x LM22	15.30	14.60	10.90	13.51	22.30	30.68	13.90	23.85	31.75	28.95	27.29	44.65	255.90	456.00	428.80	1721.00	86.20	178.90	94.10	736.00
LM13 x LM17	13.80	13.70	12.30	11.70	21.60	26.09	16.84	25.41	27.53	33.40	25.83	41.65	199.50	425.40	567.00	959.00	79.80	195.90	196.80	451.20
LM13 x LM22	14.10	17.40	12.50	11.81	17.08	26.11	19.51	22.71	28.35	30.45	26.63	43.65	292.70	470.20	544.70	958.00	82.70	212.70	209.00	461.60
LM17 x LM85	13.40	13.90	10.70	10.80	25.16	23.58	17.32	23.71	22.74	35.84	24.92	44.50	203.10	383.70	422.40	1117.00	85.80	190.00	135.30	573.10
LM22 x LM45	14.50	13.10	12.30	12.00	18.63	22.51	13.10	22.62	28.15	30.15	30.14	42.00	251.90	313.90	491.30	1031.00	88.90	125.60	145.70	425.60
Mean	13.00	13.90	11.60	11.89	22.29	22.44	14.88	22.42	28.54	34.40	26.16	40.95	170.10	359.90	580.00	1088.00	70.50	158.40	174.50	509.00
LSD (5%)	2.23	18.19	2.07	2.43	6.31	8.01	8.36	8.66	8.14	5.35	8.33	7.85	119.70	123.90	192.20	563.00	55.88	64.77	85.91	309.90
SED	1.12	9.11	1.04	1.22	3.16	4.01	4.17	4.34	4.08	2.68	4.17	3.93	59.96	62.05	96.29	282.00	27.99	32.42	43.02	155.30
CV (%)	8.09	59.34	8.76	10.45	12.34	14.78	22.80	18.44	13.28	7.62	15.56	9.08	21.19	16.59	18.70	27.41	22.92	18.51	25.94	34.22

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

3.3.3 Combining ability analysis across test environments

The combined analysis of variance for the combining ability effects and their interaction with the environments are presented in Table 3.2. The results indicated significant ($P<0.05$) site effects for all the measured traits. There were significant family effects ($P<0.05$) observed for DTH, DTM, PH, SL and KPS. GCA effects were significant ($P<0.05$) for DTH, TN, SPS, KPS, PH and SL. Also, significant ($P<0.05$) SCA effects were observed for DTH, DTM, SL and KPS. Significant ($P<0.05$) family x site effects were observed for PH only. The GCA x site effects were significant ($P<0.05$) for DTH, DTM, PH, SL, KPS, TKW. SCA x site was not significant for all the measured traits.

Table 3.2 Mean squares and significant tests for general and specific combining ability for 12 parental lines and their 66 F_3 families evaluated across drought-stressed and non-stressed conditions.

Source of variation	Df	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	BI	GY
Site	1	30.35***	9424.08***	50.10	2043.78***	8961.81***	934.60***	2818.15***	739.03***	30683941.02***	4065985.54***
Rep (Site)	2	14.77***	150.45***	3.69	15.83***	274.02***	16.56***	48.77***	25.57***	457441.62**	161343.79***
Hybrid	77	24.82***	20.58**	43.76**	1.14	153.97***	21.96	32.20***	27.99	34420.15	8861.20
GCA	11	29.50*	27.32	80.34**	1.14*	335.33***	17.10*	41.24*	35.18	39425.03	7346.35
SCA	66	9.98***	7.45**	12.43	0.47	35.24***	9.99	13.19**	10.78	13507.58	3937.06
Hybrid x Site	77	2.94	10.96	21.44*	1.02	33.71	21.04	15.03	23.05	27092.46	7200.77
GCA x Site	11	3.96***	13.54**	26.48**	0.62	34.21*	8.38	14.46*	26.10**	23306.05*	5553.82
SCA x Site	66	1.10	4.14	8.81	0.49	14.59	11.01	6.73	9.24	11919.59092	3316.08
Residual	446	2.43	14.89	16.30	1.13	32.00	22.47	19.42	65.94	71557.32	22017.93

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), Rep = replication, GCA = general combining ability, SCA = specific combining ability

3.3.4 Combining ability analysis for individual environments

Table 3.3 shows individual site analysis of variance for combining ability effects for yield and agronomic traits of bread wheat genotypes evaluated under drought-stressed and non-stressed conditions. The GCA effects were significant (P<0.05) among the genotypes for DTH, PH, SL and GY in both greenhouse and field under drought-stress. In the-non-stressed condition, GCA effects were significant (P<0.05) for DTH, DTM, PH, SL and BI in both field and greenhouse. Significant (P<0.05) GCA effects were also observed for KPS, TKW and GY in the field and TN, SPS in the greenhouse for the non-stressed condition. SCA effects under drought stress were only significant (P<0.05) for DTH (in both field and greenhouse) and DTM (in the field). Only DTH showed significant (P<0.05) SCA effects under non-stressed conditions in both field and greenhouse. In the field, SCA effects were significant (P<0.05) for DTM, TKW, BI and GY while in the greenhouse site SCA effects were only significant (P<0.05) for SL under non-stressed condition.

Table 3.3 Mean squares and significant tests in each test site and drought condition of the general and specific combining ability effects for 10 traits of 12 parental lines and their 66 F_3 families.

	Df	DTH		DTM		PH		TN		SL	
Source of variation		FIELD	GH	FIELD	GH	FIELD	GH	FIELD	GH	FIELD	GH
Drought-stressed											
GCA	11	23.49***	10.14***	35.52***	8.12	54.77***	44.72***	1.40	0.32*	309.83***	110.68***
SCA	66	8.90***	4.86***	8.41*	5.12	17.67	16.08	1.21	0.15	34.43	29.27
Residual	67	2.28	2.17	5.02	5.48	12.38	12.15	1.16	0.17	24.33	28.77
Non-stressed											
GCA	11	23.81***	12.53***	54.00***	12.17*	47.95***	94.34***	2.40	1.23**	223.56***	149.12***
SCA	66	8.72***	4.09***	14.19*	5.46	12.16	30.65	1.76	0.39	37.94	56.25*
Residual	67	1.81	1.36	9.08	5.82	12.27	21.02	1.47	0.43	27.88	34.42

Table 3.3 continued

	Df	SPS		KPS		TKW		BI		GY	
Source of variation		FIELD	GH	FIELD	GH	FIELD	GH	FIELD	GH	FIELD	GH
Drought-stressed											
GCA	11	4.51***	1.85	43.84***	20.64	60.85***	10.33	10052.47**	15064.70	2181.62**	4890.06**
SCA	66	1.1	0.80	14.59	16.31	20.98	14.74	4257.99	5438.82	1000.80	1557.21
Residual	67	1.22	1.08	9.93	16.28	16.67	17.41	3602.92	9227.93	785.91	1836.51
Non-stressed											
GCA	11	78.03	3.58*	39.29*	30.82	57.90***	19.32	8861.31*	175117.75*	3584.74***	35588.79
SCA	66	84.99	1.71	14.62	23.32	13.43**	20.11	6787.57*	79930.46	1626.89*	24661.13
Residual	67	82.45	1.48	15.79	18.18	7.18	15.57	3833.53	81826.66	1044.18	24414.81

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; SOV source of variation; df = degrees of freedom, DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), GCA = general combining ability, SCA = specific combining ability

3.3.5 GCA effects of parental lines

Table 3.4 presents the GCA effects for yield and agronomic traits of parental lines evaluated under drought-stressed and non-stressed conditions. Under drought-stressed conditions, line LM13 had the highest GCA effects for grain yield in the greenhouse. The line also recorded positive GCA effects under field condition. LM02, LM21 and LM23 had positive GCA effects for grain yield under drought-stressed condition in both sites. These lines can be candidate genetic resources for wheat improvement under drought-stressed conditions. Highest positive GCA effects for yield under drought-stress were observed for parental lines LM04 (10.79) in the field and LM13 (30.38) in the greenhouse site. Lines LM05, LM09, LM17. LM22 and LM85 showed negative GCA for grain yield under field and greenhouse conditions in undesirable direction. Under non-stressed conditions, LM04, LM13 and LM23 had large positive GCA for grain yield in both field and greenhouse environments. Lines LM09, LM21, LM22 and LM85 consistently showed negative GCA for GY under both field and greenhouse environments. Line LM02 and LM13 had several traits that had positive GCA across drought stress conditions. Across both drought and non-stressed environments, LM17 and LM85 consistently showed negative GCA for several traits recorded on both field and greenhouse conditions. LM21, LM22 and LM45 also had negative GCA for several traits under non-stressed conditions. Positive GCA effects were observed for parental lines LM09 under all test conditions for TN. Lines LM04, LM23 and LM45 showed high positive GCA effects for SL in all test conditions. Positive GCA effects for SPS and KPS were observed for lines LM04 and LM05 in both drought-stressed and non-stressed conditions. LM21 had positive GCA effects for TKW under all test conditions. Parental line LM05 showed high positive GCA effects only under non-stress conditions but low GCA effects under drought stress for BI. High positive GCA effects were observed for LM13 and LM23 in all test conditions for TN and BI. LM02 showed high positive GCA effects in all conditions except for the greenhouse site under non-stress. LM17 consistently showed low negative GCA effects across all testing conditions for DTH and PH in a desirable direction. Notably, LM17 maintained negative GCA values for all the other traits. It also showed consistent low negative GCA effects for DTM under all test conditions except for the greenhouse site under drought stress.

Table 3.4 General combining ability effects of 12 parental lines evaluated under drought-stressed and non-stressed conditions in two sites.

	DTH		DTM		PH		TN		SL		SPS		KPS		TKW		BI		GY	
Parents	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**	**Field**	**GH**
Drought-stressed																				
LM02	-0.84	-0.41	-0.52	0.15	1.98	0.40	0.25	0.00	0.99	-0.42	-0.32	-0.39	0.97	0.24	0.62	0.90	3.19	1.76	6.33	13.87
LM04	0.52	-0.15	1.48	-0.28	0.63	-0.45	-0.32	-0.06	5.86	3.73	0.78	0.02	1.91	1.72	2.85	-1.03	17.17	-9.28	10.79	-2.29
LM05	1.66	1.20	1.52	0.58	-0.33	-0.77	-0.38	-0.09	-2.85	-2.06	0.24	0.12	0.38	0.62	0.32	0.12	-12.71	-13.48	-6.04	-14.10
LM09	0.34	0.47	-0.23	-0.16	-0.81	0.86	0.20	0.09	-2.66	-0.19	-0.53	-0.04	-1.90	0.55	1.04	0.25	2.45	5.66	-0.28	-9.41
LM13	0.80	-0.35	0.84	0.92	1.33	2.83	0.15	0.15	2.44	0.67	0.54	0.51	-0.25	0.97	-0.13	0.29	13.57	54.72	0.79	30.38
LM17	-1.62	-1.03	-1.80	0.02	-1.99	-2.44	-0.19	-0.06	-2.94	-2.21	-0.47	-0.38	-0.31	-1.11	-2.05	-0.27	-41.74	-30.78	-14.35	-7.34
LM21	-0.66	-0.16	-0.20	0.14	-0.57	-0.55	0.30	0.08	-3.41	-0.96	-0.31	0.01	-0.26	-0.44	1.38	0.03	23.17	8.00	13.46	8.56
LM22	-0.87	0.17	-1.05	0.02	-0.60	0.31	-0.10	-0.02	-2.70	-2.03	-0.11	0.16	-2.41	-0.90	-1.43	0.01	-20.92	2.74	-14.34	-6.28
LM23	0.70	0.67	1.09	0.60	2.41	0.49	0.10	0.07	1.97	0.13	0.01	-0.22	0.90	-0.83	-0.34	-0.59	23.39	17.07	7.48	4.02
LM29	0.48	0.38	0.84	-0.36	0.35	-0.83	0.13	-0.18	-0.58	-0.36	0.07	-0.10	1.29	-0.01	0.43	-0.49	-0.38	-33.93	1.20	-18.02
LM45	-0.09	-0.40	-0.66	-0.97	-1.97	0.60	-0.10	0.15	5.54	3.82	0.26	0.06	-0.55	-0.71	-0.30	1.12	-4.82	7.60	-2.00	1.98
LM85	-0.41	-0.40	-1.30	-0.65	-0.43	-0.44	-0.05	-0.13	-1.66	-0.11	-0.16	0.24	0.22	-0.10	-2.38	-0.33	-2.38	-10.08	-3.02	-1.36
Non-stressed																				
LM02	-0.68	-0.05	-0.13	0.15	2.22	-0.08	-0.04	-0.18	0.80	-1.72	-1.01	-0.40	0.42	-0.71	1.89	-0.53	5.61	-49.55	7.44	-12.44
LM04	0.85	0.16	1.27	0.13	0.55	-1.38	-0.13	-0.26	6.63	4.57	0.24	0.35	1.53	2.01	2.01	1.01	33.65	-4.98	25.53	21.56
LM05	1.60	0.91	2.88	1.50	1.00	0.52	-0.29	0.30	-1.59	-1.85	3.76	0.43	2.08	0.43	-0.53	-0.04	8.78	73.23	-0.09	19.89
LM09	0.28	0.96	-0.27	0.56	-1.10	1.96	0.50	0.25	-1.00	0.75	-0.91	0.10	-1.15	-0.39	0.76	-0.14	-10.61	48.96	-6.41	-4.68
LM13	0.21	-0.23	0.27	-0.50	1.49	2.74	0.12	0.08	0.07	0.43	-0.36	0.44	-0.88	1.15	-0.84	0.35	5.86	73.31	1.43	46.53
LM17	-1.58	-1.46	-1.20	-0.86	-0.89	-1.75	0.14	-0.03	-3.91	-0.20	-1.40	-0.40	-1.48	-0.37	-0.95	-1.56	-26.76	-46.00	-10.07	0.29
LM21	-0.40	-0.51	-0.20	0.05	-1.94	-2.67	-0.05	-0.18	-0.42	-3.60	-0.59	-0.59	-0.32	-1.48	0.61	0.10	4.32	-146.33	8.14	-81.91
LM22	-0.76	0.17	-0.27	-0.44	-0.65	1.15	-0.21	0.26	-3.37	-0.82	-0.60	0.05	-1.12	0.46	-2.97	-1.31	-17.89	-5.96	-16.82	-14.55
LM23	1.39	0.72	1.52	-0.52	1.51	2.45	0.38	0.12	2.34	3.27	-0.62	0.05	1.62	-0.17	1.53	0.42	25.14	140.22	9.12	40.86
LM29	-0.11	-0.15	-2.48	0.61	-0.33	0.19	-0.59	-0.01	-0.78	-1.48	-0.75	0.29	0.11	1.10	0.01	-0.16	-14.70	42.97	-5.38	28.28
LM45	-0.36	-0.28	-0.38	-0.59	-1.16	-2.29	0.14	-0.03	2.35	1.70	-0.92	-0.36	-0.48	-1.21	-0.76	0.74	-13.81	-53.20	-8.90	-7.26
LM85	-0.43	-0.22	-1.02	-0.07	-0.68	-0.85	0.03	-0.32	-1.11	-1.05	3.16	0.05	-0.32	-0.83	-0.75	1.11	0.41	-72.67	-3.98	-36.56

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), GH = greenhouse

3.3.6 SCA effects of families

Table 3.5 summarises the SCA effects of yield and agronomic traits of F_3 bread wheat families evaluated under drought-stressed and non-stressed conditions. The top ten families all showed high positive SCA effects under field drought-stressed conditions. However, only families LM02 x LM17, LM05 x LM45, LM09 x LM45 and LM17 x LM22 maintained high positive SCA effects for grain yield under the greenhouse condition. Among these families, LM02 x LM05 and LM02 x LM17, shared a common parent that was a good general combiner under both drought-stressed and non-stressed conditions. The rest of the genotypes involved both parents that were poor general combiners for GY under drought stress. The family LM02 x LM05 consistently showed high positive SCA effect for GY in all test conditions. This is despite the fact that LM05 had negative GCA under drought stress, and LM02 had negative GCA in the green house under non-stress condition. Family LM22 x LM23 had high positive SCA effect for GY in the field but showed negative SCA effect for GY in the greenhouse under both drought-stressed and non-stressed conditions. High positive SCA effect for GY was observed for LM05 x LM22 under greenhouse non-stressed conditions (277.01) but showed negative SCA effects under drought stress. The family LM02 x LM05 maintained high positive SCA effects across all testing conditions for BI. Under drought stressed conditions families LM02 x LM17 and LM13 x LM85 showed consistently high SCA effects for BI in both sites. LM04 x LM21 showed high positive SCA effects for TKW under drought stressed conditions in both the greenhouse and field site. High positive SCA effects were observed for families LM02 x LM17 and LM22 x LM23 for KPS under drought stress conditions. The family LM22 x LM29 had high positive SCA effects for TN under both drought-stressed and non-stressed conditions. Family LM04 x LM85 maintained high positive SCA effects for SL in all test conditions. LM04 x LM22 had relatively high positive SCA effects across the test conditions for SPS. Families LM04 x LM05 and LM04 x LM45 consistently showed low negative SCA effects under drought-stressed conditions in both sites for DTH and DTM. Low negative SCA effects were observed for LM17 x LM23 across all test conditions for PH.

Table 3.5 Specific combining ability effects of 15 F_3 families obtained from a 12x12 half-diallel cross tested under drought-stressed and non-stressed conditions in the field and greenhouse sites.

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Family	DS	NS	DS	NS	DS	-NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
fifteen top families																				
LM02 x LM05	-2.07	-1.54	-1.01	0.40	-1.83	-2.54	0.60	0.42	0.70	-1.74	0.74	5.67	-0.06	0.06	0.45	-0.72	-2.99	-0.32	-0.80	3.00
LM02 x LM17	0.21	2.14	1.43	0.75	1.49	4.03	0.09	-0.12	5.46	-0.50	3.54	0.98	0.95	0.08	-0.19	0.32	2.01	1.89	-1.03	-1.08
LM02 x LM21	-0.25	-1.04	-0.81	-0.48	0.39	-1.47	-0.03	3.46	-5.31	-3.75	0.71	-4.74	-0.45	-1.82	-0.38	0.27	3.72	-1.31	4.91	-6.46
LM04 x LM09	-1.11	-0.75	-0.05	-0.16	-1.08	-1.29	-1.16	0.71	0.77	1.34	-3.63	-1.38	0.25	0.41	-0.37	0.31	1.88	1.96	-4.00	1.47
LM04 x LM13	-2.07	-1.18	-1.41	-1.89	-0.15	-3.32	0.63	0.93	-3.09	0.84	1.42	-4.85	-0.46	-0.47	-0.27	-0.32	-4.14	-5.64	2.31	-3.95
LM04 x LM85	0.14	0.96	-0.75	-0.20	0.49	1.96	-0.70	-0.01	3.31	-0.29	-1.66	-3.37	0.21	-0.02	-0.36	-0.32	9.85	0.17	2.60	0.44
LM05 x LM45	1.18	0.14	-0.39	-0.17	0.32	-0.79	0.46	0.25	0.77	4.69	-2.88	-9.42	0.56	0.03	-0.30	-1.07	6.78	1.06	0.73	-9.44
LM09 x LM23	-0.29	0.71	-0.32	-1.81	-0.68	-1.04	-2.49	0.42	0.15	-3.68	-1.27	-9.70	0.22	-1.10	-0.25	-0.37	-0.01	-4.82	-3.58	-5.03
LM09 x LM29	0.43	-1.29	-1.29	-1.20	1.57	1.46	2.09	1.19	0.44	-2.79	0.03	-1.10	1.78	1.37	0.14	-0.44	0.13	0.11	1.10	0.15
LM09 x LM45	0.00	-1.04	-0.08	-1.07	2.07	-1.15	1.88	-0.10	4.82	2.44	-0.26	0.59	-0.25	-1.70	0.15	0.08	-5.74	-1.42	-4.94	-5.54
LM13 x LM23	-0.75	-0.72	-0.53	1.38	-0.76	-2.07	1.05	0.48	7.02	1.88	-1.37	6.67	-0.35	-1.47	-0.07	0.90	4.11	2.02	-0.03	9.70
LM13 x LM85	-1.14	-2.40	1.37	-0.92	0.14	-1.54	1.00	1.12	-0.19	-0.29	-2.28	0.46	0.49	0.23	0.37	0.14	1.52	-2.63	-4.24	-4.98
LM21 x LM45	1.50	1.53	0.56	1.66	1.78	1.60	0.62	-0.43	5.11	-3.04	1.18	1.80	0.96	-0.70	0.03	0.27	3.26	-2.37	-0.36	4.43
LM22x LM23	1.50	0.64	0.44	0.86	1.53	1.28	-0.65	-2.50	-1.55	-1.87	2.29	3.17	-0.36	0.60	0.16	0.41	1.43	-1.69	1.00	1.48
LM23 x LM45	-1.07	-3.75	-0.66	-2.48	1.64	-0.54	-0.89	1.95	2.37	0.52	1.35	-0.49	0.42	-1.14	-0.49	-0.28	-0.32	4.53	2.13	-4.00
five bottom genotypes																				
LM05 x LM22	5.46	7.03	6.10	4.13	6.21	8.10	-0.51	3.16	0.01	-0.12	-0.46	5.39	-0.85	0.59	-0.53	0.74	6.00	0.72	-3.89	4.73
LM13 x LM17	1.57	1.25	1.11	-0.21	0.64	1.64	0.89	1.48	-3.74	2.38	3.48	-0.44	-1.84	1.02	0.10	-0.65	1.00	-4.51	-3.50	-1.04
LM13 x LM22	-0.68	0.43	-2.54	-1.22	0.39	1.21	-0.62	-0.36	-5.27	2.64	-1.24	0.57	-0.65	0.72	0.05	-0.14	-7.64	0.39	-2.65	-8.06
LM17 x LM85	-1.21	-0.61	-0.70	-1.31	-3.22	-1.07	-1.85	-1.06	-1.13	-0.60	0.99	3.35	0.69	0.56	-0.13	0.25	2.60	1.85	0.77	3.06
LM22 x LM45	-2.29	-1.50	-0.59	0.60	-1.11	-2.65	0.18	-1.57	0.10	0.74	2.59	1.65	-0.21	0.45	0.13	-0.23	7.35	-4.91	-1.77	3.19

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), GH = greenhouse, DS = drought-stressed, NS = non-stressed

Table 3.5 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Entry	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
fifteen top families																				
LM02 x LM05	0.16	-3.72	-0.20	0.12	-0.36	6.51	4.42	8.82	2.24	-1.11	-0.78	1.99	51.98	19.34	100.75	145.07	37.99	21.61	73.29	117.79
LM02 x LM17	0.78	0.36	0.26	-0.48	6.05	1.52	4.61	-2.30	4.92	2.12	-1.84	-0.75	67.02	10.48	14.08	-31.68	37.51	1.80	12.85	-47.72
LM02 x LM21	0.32	-0.54	0.28	-1.55	1.60	1.41	2.72	-3.84	1.68	-5.68	1.71	-0.12	30.19	-5.40	-41.28	-153.19	20.76	-16.99	-5.40	-70.14
LM04 x LM09	-0.16	0.21	-1.25	-0.65	1.31	-0.95	2.58	0.77	2.43	-0.21	-0.80	1.69	13.60	-15.06	-72.57	91.77	15.06	-5.38	-25.01	88.42
LM04 x LM13	-0.93	-0.69	0.67	-0.74	2.83	-0.46	-0.83	-3.11	1.63	-4.40	1.51	0.73	14.86	-74.53	-19.56	-279.78	9.96	-51.34	-24.19	-163.41
LM04 x LM85	1.26	-3.43	-0.14	-0.37	-1.06	8.99	0.70	0.30	4.82	4.01	0.03	-0.71	93.47	46.90	-6.04	-102.61	42.86	24.87	-4.02	-36.25
LM05 x LM45	1.28	-2.07	-0.50	-0.31	1.68	-1.34	1.23	-1.69	3.23	-0.57	-1.91	-1.30	70.15	89.26	-32.99	-354.76	40.89	31.68	9.04	-132.78
LM09 x LM23	0.91	-0.80	0.20	-1.03	-0.92	-1.24	-2.27	-1.67	-0.31	-4.33	-1.17	1.20	17.11	-79.54	-24.24	-252.14	12.01	-33.07	-22.03	-75.56
LM09 x LM29	-0.15	0.85	0.50	0.84	-1.83	0.44	-4.35	1.59	1.40	0.14	2.06	2.08	98.90	-13.41	-3.09	-94.97	38.12	-0.80	-3.99	-43.13
LM09 x LM45	-0.24	1.12	0.22	0.40	1.50	0.32	0.29	-3.08	2.48	1.16	3.35	-0.22	26.46	4.04	27.11	-249.55	27.62	13.99	42.36	-135.77
LM13 x LM23	0.14	0.48	0.53	1.62	-0.68	-0.10	-0.31	1.38	2.82	1.59	-1.43	0.51	55.37	-14.46	-16.43	144.24	18.08	-4.47	-20.07	61.42
LM13 x LM85	0.50	-4.05	-0.16	-0.44	0.70	-2.28	-3.07	3.67	2.32	-0.41	3.55	1.49	64.32	-18.45	31.36	26.69	33.53	-17.00	-3.28	28.43
LM21 x LM45	0.04	-0.43	0.11	-0.13	2.53	0.08	1.01	4.05	-0.99	-0.49	-2.93	-6.71	36.87	-5.43	55.51	179.54	21.48	-1.40	7.58	106.62
LM22x LM23	0.18	1.29	0.20	-0.05	3.79	4.39	4.12	1.35	5.46	3.12	-1.18	-0.95	129.48	62.92	-68.72	-122.88	70.51	38.99	-17.09	-66.69
LM23 x LM45	-0.19	0.41	-0.47	0.23	0.43	4.71	-1.01	4.22	2.93	-1.66	0.03	-0.73	26.05	-47.74	6.30	46.47	14.26	-24.64	-11.15	81.68
five bottom families																				
LM05 x LM22	1.35	-3.90	-0.69	1.32	-1.41	2.68	-4.18	-0.23	1.80	-2.70	-1.19	2.70	-0.05	95.18	-70.22	624.47	-19.61	20.27	-55.34	277.01
LM13 x LM17	-0.08	-0.62	0.01	-0.03	-3.46	1.39	-1.21	1.47	-2.13	0.01	-0.38	-0.92	-74.36	49.33	57.45	-97.70	-34.34	19.42	16.59	-49.31
LM13 x LM22	-0.15	3.69	0.12	-0.40	-5.90	1.05	1.25	-2.32	-0.50	-1.16	-2.03	1.21	31.20	117.06	-25.24	-137.92	-19.76	55.57	18.17	-24.05
LM17 x LM85	0.21	-3.27	-0.87	-0.53	-0.16	-1.67	0.33	0.94	-2.50	2.22	-2.58	1.62	9.72	37.15	-34.89	206.56	-4.34	27.31	-18.68	155.72
LM22 x LM45	0.53	-0.75	0.11	0.63	-4.09	-2.92	-3.53	-0.13	-1.06	-1.56	1.91	-0.16	-15.17	-55.05	-19.54	60.75	-20.00	-39.50	-15.42	-6.24

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), GH = greenhouse, DS = drought-stressed, NS = non-stressed

3.3.7 Variance components

Variance components, heritability and the GCA/SCA ratio for yield and agronomic traits of F_3 bread wheat genotypes evaluated under drought-stressed and non-stressed conditions are presented in Table 3.6. Higher values for variance due to SCA than variance due to GCA were observed for DTH, DTM, PH, TN, SPS, KPS, TKW and BI in both sites under both water regimes. Both variances due to GCA and SCA were higher for field experiments for most traits, across drought-stressed and non-stressed conditions. SL showed higher values for variance due to GCA than SCA in all test environments except the greenhouse site under non-stressed condition. The GCA/SCA ratio was below a unit for all the traits under drought-stressed and non-stressed conditions. However, GY under greenhouse non-stressed conditions, KPS under greenhouse drought-stressed conditions and SL under drought stressed conditions showed GCA/SCA ratio values approaching a unit. Broad sense heritability ranged from 0 (TKW) to 68% (DTH) under drought stressed conditions and from 2% (SPS) to 73% (DTH) under non-stressed conditions. Narrow sense heritability ranged from 0% for TKW to 41% for SL and 0 for SPS to 30% for SL under drought-stressed and non-stressed conditions, respectively.

Table 3.6 Variance components based on combining ability and heritability for 10 traits of 12 parents and 66 F_3 families evaluated under drought-stressed and non-stressed conditions under field and greenhouse conditions.

Trait	Site	σ^2_{gca}	σ^2_{sca}	GCA/SCA	σ^2_p	h^2	H^2
				Drought stress			
DTH	Field	0.76	3.31	0.31	7.10	0.21	0.68
	GH	0.28	1.34	0.30	4.08	0.14	0.47
DTM	Field	1.09	1.70	0.56	8.89	0.24	0.44
	GH	0.09	0.00	-	5.67	0.03	0.03
PH	Field	1.51	2.65	0.53	18.05	0.17	0.31
	GH	1.16	1.96	0.54	16.44	0.14	0.26
TN	Field	0.01	0.03	0.40	1.20	0.01	0.04
	GH	0.01	0.00	-	0.18	0.06	0.06
SL	Field	10.20	5.05	0.80	49.77	0.41	0.51
	GH	2.93	0.25	0.96	34.87	0.17	0.18
SPS	Field	0.12	0.00	-	1.46	0.16	0.16
	GH	0.03	0.00	-	1.13	0.05	0.05
KPS	Field	1.21	2.33	0.51	14.68	0.16	0.32
	GH	0.16	0.01	0.96	16.60	0.02	0.02
TKW	Field	1.58	2.16	0.59	21.98	0.14	0.24
	GH	0.00	0.00	-	17.41	0.00	0.00
BI	Field	230.34	327.53	0.58	4391.13	0.10	0.18
	GH	208.46	0.00	-	9644.84	0.04	0.04
GY	Field	49.85	107.45	0.48	993.05	0.10	0.21
	GH	109.06	0.00	-	2054.62	0.11	0.11
				Non-stress			
DTH	Field	0.79	3.45	0.31	6.84	0.23	0.73
	GH	0.40	1.37	0.37	3.52	0.23	0.62
DTM	Field	1.60	2.55	0.56	14.85	0.22	0.39
	GH	0.23	0.00	-	6.28	0.07	0.07
PH	Field	1.27	0.00	-	14.82	0.17	0.17
	GH	2.62	4.82	0.52	31.07	0.17	0.32
TN	Field	0.03	0.15	0.31	1.68	0.04	0.13
	GH	0.03	0.00	-	0.49	0.12	0.12
SL	Field	6.99	5.03	0.74	46.89	0.30	0.41
	GH	4.10	10.92	0.43	53.53	0.15	0.36
SPS	Field	0.00	1.27	0.00	83.72	0.00	0.02
	GH	0.08	0.11	0.57	1.74	0.09	0.15
KPS	Field	0.84	0.00	-	17.46	0.10	0.10
	GH	0.45	2.57	0.26	21.65	0.04	0.16
TKW	Field	1.81	3.13	0.54	13.93	0.26	0.48
	GH	0.13	2.27	0.11	18.11	0.01	0.14
BI	Field	179.56	1477.02	0.20	5669.67	0.06	0.32
	GH	3331.82	0.00	-	88490.31	0.08	0.08
GY	Field	90.73	291.35	0.38	1517.00	0.12	0.31
	GH	399.07	123.16	0.87	25336.11	0.03	0.04

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m2), GY = grain yield (g/m2), GCA = general combining ability, SCA = specific combining ability, σ^2_{gca} = variance due to GCA , σ^2_{sca} = variance due to SCA, σ^2_p = phenotypic variance, h^2 = narrow sense heritability, H^2 = broad sense heritability, GH = greenhouse

3.4 Discussion

3.4.1 Analysis of variance

Highly significant differences were observed for most of the yield and agronomic traits for genotypes and sites indicating the presence of genetic variation among the genotypes and the impact of different sites on performance. Drought stress affected the performance of genotypes as reflected by significant effects of drought conditions on the performance of the traits. Similar results of reduced yield and yield components have been reported by Sher et al. (2017) and Wang et al. (2017) under drought stress.

3.4.2 Mean grain yield and agronomic performance of parents and families

There is increased need to identify and characterize lines and families under drought- and non-stressed conditions. Generally, drought stress reduced the performance of all the traits (Table 3.1) with GY incurring losses of 55% and 66% under greenhouse and field conditions respectively. This is because of the negative impact of drought on the physiological and biochemical process in plants which leads to decreased cell enlargement and reduced plant growth (Jaleel et al., 2009). The top performing families including LM02 x LM21 and LM04 x LM13 had low DTH and high DTM indicating a longer grain filling period than the bottom performing genotypes which had high DTH values. This could have contributed to higher yields observed in the top performing families as higher grain filling is associated with enhanced grain yield (Hunt et al., 1991). The better yielding genotypes including LM02 x LM05, LM02 x LM21, LM04 x LM85, LM05 x LM45 and LM22 x LM23 had corresponding high values for SL, KPS, TKW and BI suggesting that these traits contributed substantially to better yield performance. This agrees with Fang et al. (2017) who attributed improved grain yield of new cultivars to the improvement of number of kernels per spike and thousand kernel weight. Furthermore, Golparvar (2014) reports the importance of increased biomass under drought stress and recommends the use of the trait for selection in stress environments. The bottom five families (Table 3.1) notably performed well under non-stress conditions, but experienced yield losses of over 50% due to drought-stressed conditions under field conditions. This indicates that high performance under optimum moisture conditions does not always translate to better performance under stress conditions but depends on the genetic makeup of the genotypes (Rampino et al., 2006).

3.4.3 Analysis of variance based on combining ability

Combining ability analysis is important in revealing the mode of gene action that is predominant in controlling plant traits. This information is vital in implementing breeding strategies that result in successful crop improvement. The combined analysis of variance across sites (Table 3.2) revealed significant effects for GCA x site interaction for DTH, DTM, PH, SL, KPS, TKW and BI indicating that the mode of gene action that was governing these traits was influenced by sites and drought stress. The analysis of variance for individual sites (Table 3.3) revealed high GCA effects under drought-stress for GY, DTH, PH and SL across all test conditions indicating the influence of additive gene action in the inheritance of these traits. For these traits, exploitation of additive gene action by direct selection of families which perform well for these traits will lead to genetic gains being realised in water limited environments (Farshadfar et al., 2011). Significant GCA effects for DTM, SPS, KPS, TKW and BI in the field and TN in the greenhouse under drought-stressed conditions also indicates the influence of additive gene action in the inheritance of these traits in those conditions. Significant SCA effects under drought-stress were only observed for DTH and DTM in the field signifying the influence of non-additive gene action. The significance of both GCA and SCA effects for DTH in all test conditions showed that DTH is under the control of both additive and non-additive gene action (Susanto, 2018). Under non-stressed conditions DTH, DTM, PH, SL and BI showed the influence of additive gene action in the field and greenhouse sites as shown by significant GCA effects. Significant SCA effects for DTM in both the greenhouse and field sites, for DTM, TKW, BI and GY in the field only and SL in the greenhouse under non-stressed conditions signify the influence of non-additive gene action under the respective conditions.

3.4.4 General combining ability effects

The GCA of parental lines reveals their breeding value which can be exploited in plant breeding programs to produce families that perform better than their parents. Parental line LM05 showed consistently positive GCA effects for BI and GY under non-stressed conditions but consistently low negative GCA effects under drought stressed conditions (Table 3.4). According to Becker and Leon (1988) and Fang et al. (2017), a successful genotype should be able to maintain a high yield performance across multiple environments and should possess tolerance to different stresses including drought stress. This shows that parent LM05 is less stable across varying moisture levels, severely affected by drought and cannot be utilized for improved drought tolerance. Therefore, it should be utilised in plant breeding programs that target wheat production under optimum moisture growing conditions. Parental lines LM02, LM13 and LM23 consistently showed high positive GCA effects for GY in all the test environments showing their utility as sources of additive genes for yield under both non-stressed and drought-stressed conditions, as well as stability across varying moisture conditions. This agrees with Fleury et al. (2010) who states that drought tolerant genotypes should be able to perform well under drought stress and match high yielding genotypes in optimum growing conditions. Lines LM13 and LM23 can be of great value in breeding programs as they also showed high GCA values for BI and TN in all test conditions and can be utilised to improve these traits simultaneously under both drought-stressed and non-stressed conditions. An increase in TN and BI can be used for indirect improvement in grain yield as these traits have been shown to be positively correlated with GY under both non-stressed and drought-stressed conditions (Ali et al., 2015; Naghavi et al., 2015). Ali et al. (2015) also showed that TKW was positively correlated with grain yield in drought-stressed conditions and thus lines LM13 and LM23 can be used to transfer additive genes for TKW as they constantly showed high positive GCA effects in all test environments. Negative GCA values are desired when selecting for DTH and DTM under terminal drought-stress because early heading and maturity allow for drought escape by completion of the plants lifecycle before severe drought sets in (Shavrukov et al., 2017). Parental line LM17, a good general combiner for DTH, DTM and PH can be used to transfer genes for earliness and reduced height as it continuously showed low negative GCA for these traits. However, line LM17 showed consistently negative GCA values for BI and GY under drought-stress which indicates that earliness in this line led to a yield penalty due to reduced photo-assimilate production because of hastened maturity and low biomass production (Zaharieva et al., 2001; Shavrukov et al., 2017). Parental line LM04 and LM05 showed consistently high positive GCA values for SPS and KPS which are associated with high grain yield as reported by Eid (2009). Selection for these traits can be used to increase the kernel number under drought stress which can compensate for yield loss due to reduced kernel weight.

3.4.5 Specific combining ability effects

Information on the specific combining ability of crosses and families can be used to aid the identification of families that can produce transgressive segregants in later generations (Kumar et al., 2017). High positive SCA effects (Table 3.5) for BI and GY in all test environments were observed for LM02 x LM05. Families LM05 x LM45, LM02 x LM17, LM09 x LM45 and LM17 x LM22 showed high SCA effects for GY under drought-stressed conditions. Families LM02 x LM05 and LM02 x LM17 involve at least one parent (LM02), with consistent positive GCA values in the varying test environments for both BI and GY suggesting the accumulation of favourable genes for these traits in these families (Ababulgu, 2014). The families LM05 x LM45, LM09 x LM45 and LM17 x LM22 showed greater performance for GY involving poor general combiners for grain yield under drought indicating the presence of non-additive gene effects probably with complementary epistatic interactions (Dey et al., 2014).

Therefore, selection at this stage will not be effective in fixing high yield in these families (Patel et al., 2018). The high positive SCA effects for LM22 x LM23 for GY in the field coupled with low negative SCA effects in the greenhouse show the impact of the two different sites on expression of grain yield. This is because combining ability effects of GY are affected by genotype x environment interactions due to the polygenic nature of the trait (Fasahat et al., 2016). Low negative SCA effects were observed for LM04 x LM05 and LM04 x LM45 for DTH and DTM indicating the effect of non-additive gene action especially for family LM04 x LM05 as both parents were poor general combiners for reduced DTH and DTM. Families LM22 x LM29 for TN, LM04 x LM85 for SL, LM04 x LM22 for SPS, LM04 x LM21 for TKW showed positive SCA effects reflecting the prevalence of non-additive gene action in expression of these traits in these families.

3.4.6 Gene action

The GCA/SCA ratio showed values less than unity for all the measured traits signifying the predominance of non-additive gene action in the inheritance of these traits under both stressed and non-stressed conditions (Table 3.6). This agrees with the results of Saeed et al. (2010) under both drought-stressed and non-stressed conditions and Saeed and Khalil (2017) under rainfed growing conditions. However, SL showed GCA/SCA ratio values close to a unity (≥0.80) under drought stress signifying the influence of additive gene effects for control of the trait under drought-stressed conditions. Of all the studied traits, SL scored moderate heritability ($0.40 \leq h^2 \leq 0.50$) in the narrow sense under drought-stress indicating that fixable genetic variation governs this trait (Saeed and Khalil, 2017). This moderate heritability combined with the predominance of additive gene action in the inheritance of SL present it as a valuable trait that can be used for selection by accumulating additive gene effects leading to successful selection (Fasahat et al., 2016).

3.5 Conclusions

The F_3 families showed significant variation in the mean squares for GCA effects for all the traits in at least one test environment. Significant SCA effects were only observed for DTH in test conditions and sites. Significant SCA effects were also observed for DTM in the field under both drought-stressed and non-stressed conditions and for GY in the field under non-stressed conditions. The GCA/SCA ratio for all the traits were below unity indicating predominance of non-additive gene action in the control of the measured traits. Broad-sense heritability and narrow-sense heritability were generally low for all the traits with moderate heritability in the narrow sense being observed for SL under drought-stressed conditions. The results indicated that LM17 is a good general combiner for reduced DTH, DTM and PH which are useful traits in drought tolerant wheat genotypes. Lines LM02, LM13 and LM23 were good general combiners for GY and can be used to improve wheat genotypes for GY in both drought-stressed and non-stressed conditions in well-designed crosses. LM23 was also a good general combiner for several other traits including TN, SL and TKW. LM02 x LM05 and LM02 x LM17 are recommended for advancing to F_4 generation for further selection as they had high SCA effects in the presence of at least one good general combiner indicating the presence of additive x additive gene interactions which can be fixed in later generations.

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Appendix 3.1 Mean performance for 10 agronomic traits of 66 families and 12 parents in two testing sites under drought-stressed and non-stressed conditions.

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM02XLM04	49.00	50.50	51.00	48.00	76.50	82.50	83.00	88.00	65.85	62.55	59.60	58.00	4.95	6.55	1.60	2.10	82.99	78.20	66.80	64.40
LM02XLM05	49.50	49.50	50.00	50.50	76.50	80.50	85.00	91.50	64.25	64.25	61.40	68.10	5.25	5.95	2.00	2.20	71.02	77.90	64.40	68.30
LM02XLM09	47.50	48.00	49.50	50.00	72.50	78.00	86.50	89.50	63.70	62.40	53.80	66.35	6.15	7.65	1.50	3.70	75.64	80.40	60.50	79.20
LM02XLM13	48.00	49.50	49.00	48.00	75.50	80.00	83.00	86.00	65.65	66.00	63.40	66.50	6.00	6.10	1.80	2.60	79.89	83.00	69.90	70.10
LM02XLM17	48.50	50.00	50.50	48.00	76.50	83.00	84.50	89.00	67.35	63.60	62.75	61.15	6.45	6.40	1.50	2.90	75.92	79.60	63.70	66.10
LM02XLM21	49.00	48.00	49.00	48.00	77.00	78.50	84.00	93.00	57.25	59.30	62.05	54.50	5.65	4.30	1.50	2.70	78.64	77.60	71.00	57.60
LM02XLM22	48.00	47.50	48.50	48.50	73.00	78.50	85.00	88.50	60.95	62.75	60.10	54.35	4.60	5.90	1.60	2.20	75.10	74.10	65.40	55.20
LM02XLM23	52.00	52.00	50.50	50.00	78.50	82.50	84.50	89.00	66.20	69.75	65.10	66.95	5.10	7.55	1.90	2.70	81.00	87.80	70.40	77.70
LM02XLM29	52.50	50.00	51.00	49.00	82.00	81.50	85.50	92.50	62.95	67.80	54.10	60.05	7.00	5.50	1.30	2.80	82.61	82.60	59.20	61.70
LM02XLM45	51.00	48.50	49.00	48.00	77.50	76.50	82.50	88.50	61.15	65.80	56.45	59.15	5.95	5.50	1.60	2.80	75.10	78.20	65.40	71.50
LM02XLM85	52.00	50.50	50.50	50.00	77.50	78.50	80.50	89.50	59.80	66.10	62.25	62.00	6.65	6.40	1.80	1.90	76.06	79.00	70.40	71.90
LM04XLM05	49.00	48.00	49.00	48.00	77.50	82.50	85.00	92.00	61.80	65.85	61.95	62.20	5.45	6.10	1.30	2.70	77.59	81.40	70.40	68.00
LM04XLM09	50.50	50.50	50.50	50.00	77.50	80.00	81.50	91.00	62.35	63.55	55.15	61.20	5.60	7.00	1.20	3.10	82.00	87.00	66.00	75.80
LM04XLM13	50.00	50.00	48.50	46.50	79.50	78.50	85.00	89.50	60.30	65.65	65.15	58.50	4.85	5.75	1.50	2.30	80.61	79.20	74.20	69.90
LM04XLM17	49.50	47.50	49.00	47.00	76.50	78.00	82.50	90.50	63.15	66.10	60.45	60.05	5.40	6.40	1.80	2.70	75.61	78.90	68.60	71.60
LM04XLM21	50.00	50.00	48.50	49.00	78.00	81.50	83.50	88.00	62.35	57.40	59.45	58.85	5.55	5.50	1.90	2.40	78.50	85.50	71.50	70.70
LM04XLM22	48.00	48.50	50.50	48.50	77.50	79.50	83.00	89.50	59.35	60.80	61.55	61.70	5.65	4.55	2.10	2.60	81.32	81.90	69.80	81.10
LM04XLM23	55.50	58.00	52.50	54.50	82.00	90.00	85.50	88.50	63.75	64.95	52.65	71.90	5.25	6.20	1.40	2.70	87.22	96.10	68.80	84.80
LM04XLM29	53.50	50.50	52.00	50.50	80.00	80.50	82.50	92.00	63.10	63.40	57.80	56.70	5.15	4.55	1.90	3.20	86.52	88.40	73.80	71.50
LM04XLM45	48.00	47.50	47.00	47.00	77.00	78.00	79.00	88.00	55.40	60.00	55.15	58.30	4.35	4.75	1.20	2.40	85.11	86.70	72.10	72.90
LM04XLM85	51.00	51.50	49.50	49.00	78.00	82.50	80.50	89.50	64.95	62.35	58.95	56.40	5.25	6.10	1.20	1.90	90.13	85.10	74.60	73.10
LM05XLM09	50.50	54.00	51.00	50.00	76.50	82.50	80.00	89.00	63.20	63.10	62.10	66.80	5.00	6.50	1.70	2.90	69.21	81.50	73.90	71.30
LM05XLM13	54.00	51.50	50.00	50.00	80.50	83.50	85.00	90.50	62.85	66.40	62.20	63.80	7.00	6.70	1.90	3.40	73.69	81.80	63.20	72.40
LM05XLM17	51.00	48.50	49.00	49.00	79.00	78.00	82.00	90.00	57.30	67.20	54.15	60.85	4.49	5.10	1.80	2.80	65.02	78.40	75.80	68.80
LM05XLM21	50.00	49.50	50.00	48.00	76.50	78.50	84.50	91.50	54.85	61.65	58.75	59.95	6.25	5.70	2.30	2.90	67.26	74.00	59.10	64.90
LM05XLM22	57.00	58.00	57.50	54.00	84.00	91.00	85.00	93.00	61.40	63.00	57.55	69.05	4.10	6.30	0.90	4.10	77.31	73.90	57.60	71.20
LM05XLM23	52.50	54.00	53.00	50.00	79.50	85.50	85.00	88.00	62.00	62.95	61.10	60.80	5.85	7.10	1.80	3.60	69.51	67.80	58.70	60.00
LM05XLM29	51.00	49.50	51.50	49.00	79.50	80.50	80.00	92.00	61.45	63.65	58.00	66.20	4.50	5.45	1.00	2.80	77.21	74.10	62.20	65.80
LM05XLM45	53.50	51.50	51.00	49.50	78.50	82.00	84.00	90.50	60.30	67.30	58.55	50.80	5.55	6.10	1.50	2.00	86.61	80.60	70.00	59.80
LM05XLM85	50.00	49.00	49.50	48.00	76.50	78.50	83.00	90.00	64.15	61.45	56.75	59.40	4.60	5.55	1.40	2.80	66.49	72.90	63.60	64.20
LM09XLM13	56.50	49.50	51.00	50.50	81.50	79.50	85.00	91.50	57.65	62.40	65.75	67.55	5.95	5.80	2.20	3.50	81.40	74.40	66.90	73.10
LM09XLM17	48.50	48.00	49.00	47.00	75.50	79.00	82.00	91.50	59.95	58.75	61.55	62.80	5.00	6.25	1.90	2.90	72.40	75.90	71.00	70.50
LM09XLM21	48.50	48.00	50.00	48.50	76.00	78.50	80.50	90.00	58.25	60.45	63.90	60.60	5.25	7.15	1.80	2.80	74.20	74.30	65.70	60.70

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**
LM09XLM22	50.50	49.50	52.00	51.00	76.00	83.00	82.00	91.00	62.10	65.60	66.60	70.70	4.49	6.75	2.00	3.80	71.31	78.10	65.90	72.90
LM09XLM23	51.50	52.50	51.00	49.00	77.50	80.50	79.50	90.00	63.65	59.50	60.60	56.70	5.97	6.00	1.50	2.80	76.61	75.30	64.70	68.20
LM09XLM29	52.00	49.00	50.00	49.00	79.50	79.00	85.50	92.00	62.00	58.55	60.10	63.05	7.60	7.50	1.70	2.60	74.20	76.40	67.45	68.50
LM09XLM45	51.00	49.00	50.50	49.00	78.50	78.50	84.50	89.50	63.55	62.95	62.55	62.25	5.25	5.15	2.20	3.10	73.71	78.00	66.30	66.00
LM09XLM85	51.50	51.50	53.50	50.50	79.00	80.50	85.00	90.50	60.25	63.15	61.95	59.40	6.80	6.55	1.80	2.70	72.22	75.60	70.50	62.10
LM13XLM17	51.50	50.00	50.50	47.00	77.00	81.00	84.50	90.50	57.50	65.75	63.90	62.55	3.57	7.50	1.80	2.20	77.81	71.60	62.10	68.10
LM13XLM21	48.00	49.50	50.00	46.50	73.00	81.00	84.50	86.00	63.05	65.15	61.85	58.40	6.25	7.85	1.80	1.90	78.91	76.30	64.20	68.30
LM13XLM22	50.00	50.00	48.00	48.00	77.50	81.50	84.50	88.50	57.00	66.25	62.50	66.45	4.95	6.85	1.80	3.00	69.70	76.10	62.60	60.40
LM13XLM23	51.50	51.00	50.50	51.00	78.50	80.00	85.00	89.00	72.75	67.65	63.10	73.85	5.35	5.25	1.90	3.90	86.11	83.80	69.00	82.60
LM13XLM29	53.00	51.00	52.00	50.00	78.00	80.00	84.00	90.50	65.45	62.80	65.75	66.75	5.25	5.75	1.90	2.80	77.52	75.70	70.30	71.25
LM13XLM45	50.50	50.00	49.50	48.00	77.00	82.50	85.00	88.50	64.90	66.20	65.30	64.55	6.00	7.20	1.70	3.00	87.40	90.60	76.20	79.40
LM13XLM85	50.00	47.50	51.00	48.00	77.00	78.00	85.00	90.00	62.35	63.30	61.60	64.35	6.10	6.60	2.20	2.70	79.32	75.50	63.80	63.70
LM17XLM21	49.00	49.00	50.00	47.50	75.50	80.00	86.00	85.00	62.60	58.00	51.75	63.10	6.50	7.20	1.40	3.10	66.85	75.20	60.70	68.60
LM17XLM22	47.50	47.50	50.00	46.50	74.00	78.00	84.00	89.50	57.65	60.00	58.05	60.35	4.80	5.05	1.80	3.60	68.12	70.90	63.30	63.40
LM17XLM23	48.00	47.00	50.00	46.50	73.50	76.50	87.50	87.50	54.80	62.25	50.90	59.40	4.90	6.35	1.20	2.40	71.46	71.50	55.70	65.20
LM17XLM29	49.50	48.00	49.50	48.00	76.00	78.00	80.00	88.00	54.00	65.10	60.05	61.65	3.90	6.50	1.20	2.70	74.70	78.50	66.00	74.20
LM17XLM45	48.50	49.50	48.50	48.00	74.50	79.50	82.00	89.50	55.05	60.30	57.40	46.20	5.45	7.50	2.00	1.90	85.81	80.10	65.20	60.80
LM17XLM85	47.50	47.50	48.50	46.00	71.00	77.00	82.00	87.00	58.05	60.60	58.35	62.75	5.95	6.95	1.30	2.70	74.34	76.20	64.90	71.20
LM21XLM22	50.00	49.50	52.50	48.50	75.50	78.00	85.00	90.50	63.90	60.85	61.35	58.85	5.40	5.10	1.80	2.50	72.39	82.50	62.90	63.30
LM21XLM23	51.50	51.50	50.50	49.00	79.50	82.00	84.00	91.00	66.60	64.25	61.00	56.45	5.65	7.75	1.90	2.20	71.39	79.00	65.90	65.90
LM21XLM29	48.50	50.50	50.00	48.00	77.50	79.50	82.00	89.50	62.60	59.45	62.45	62.85	5.00	5.00	1.70	2.60	75.01	82.30	68.40	65.50
LM21XLM45	51.50	50.00	50.50	49.00	78.00	81.00	83.00	86.50	57.65	57.80	62.60	60.20	5.45	6.90	2.00	3.00	80.08	79.85	70.30	68.30
LM21XLM85	50.50	48.50	49.50	49.00	77.00	79.50	85.00	91.50	62.45	62.20	60.50	55.90	5.45	5.50	1.60	2.10	70.54	82.20	67.00	63.80
LM22XLM23	49.50	47.00	51.00	47.50	79.00	81.00	84.50	90.00	66.50	64.15	62.70	65.10	5.85	5.25	1.20	2.90	75.81	82.00	66.70	68.00
LM22XLM29	50.75	50.12	50.50	49.00	77.33	80.29	83.61	89.55	61.66	62.77	60.52	61.99	5.48	6.22	1.66	2.80	76.76	78.99	67.09	69.01
LM22XLM45	47.50	47.50	50.00	49.50	74.50	77.00	84.00	87.00	59.75	61.70	64.05	62.50	5.10	6.60	1.90	2.80	86.90	72.80	66.50	72.80
LM22XLM85	48.50	47.50	46.50	49.00	75.00	79.00	82.50	87.00	58.20	58.80	56.10	62.35	5.90	7.40	1.40	2.50	65.89	70.40	59.30	72.00
LM23XLM29	51.50	50.00	51.00	50.00	79.50	80.50	85.50	90.00	65.65	63.20	62.60	63.50	6.45	5.10	1.50	2.60	77.79	83.50	73.10	75.30
LM23XLM45	50.00	51.00	50.50	47.00	78.50	81.00	82.00	88.00	62.65	59.45	61.90	62.35	5.80	9.90	2.00	2.80	85.61	86.40	74.50	72.80
LM23XLM85	49.00	49.00	51.00	48.50	73.50	78.50	83.50	86.50	61.05	66.55	59.55	64.25	4.65	6.70	1.90	2.50	78.10	77.80	62.90	69.80
LM29XLM45	50.00	49.00	51.00	48.00	75.00	78.50	84.50	90.50	58.45	61.80	63.80	61.20	4.90	6.30	1.70	2.30	71.60	75.30	70.30	69.10
LM29XLM85	51.00	49.00	51.00	48.00	77.50	78.50	87.00	90.50	63.00	63.70	58.00	57.95	5.50	5.35	0.80	2.80	71.80	79.70	60.60	67.40
LM45XLM85	48.00	48.00	50.00	47.50	73.00	79.00	82.50	90.50	57.25	60.80	60.15	62.80	5.35	5.50	1.60	2.70	77.71	77.80	76.10	71.40

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Parents	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**
LM02	50.50	49.00	51.00	49.00	77.50	81.00	86.00	91.00	67.60	68.40	64.30	63.85	5.70	6.20	1.50	2.60	79.20	80.70	66.90	65.10
LM04	56.50	55.50	53.00	51.00	83.00	84.00	81.50	89.50	63.30	65.55	64.05	61.40	4.45	7.80	1.60	2.30	85.11	96.20	75.20	78.60
LM05	57.50	55.50	56.00	52.00	81.00	90.50	86.50	93.00	61.90	61.65	63.80	62.60	3.85	5.10	1.60	4.20	77.52	77.50	64.50	68.30
LM09	53.00	53.00	52.50	53.50	76.00	80.50	84.50	89.00	57.45	60.10	64.45	68.00	5.40	7.75	2.00	3.00	69.92	78.70	68.00	69.20
LM13	54.00	52.50	51.00	50.00	81.00	81.00	84.50	89.00	65.10	59.70	66.90	65.50	6.15	5.60	2.00	3.10	80.05	80.10	71.50	61.30
LM17	49.00	48.50	49.50	47.50	75.50	79.50	85.50	87.00	62.55	57.95	57.15	60.30	6.05	5.80	1.60	3.00	73.81	68.30	61.50	73.30
LM21	52.00	51.00	52.00	49.00	79.50	81.50	84.00	91.00	60.65	61.20	59.25	59.40	6.75	6.05	1.80	2.80	67.95	73.90	66.60	63.90
LM22	51.00	50.00	51.00	50.00	74.50	77.50	80.50	87.50	64.60	62.15	59.35	63.50	5.75	6.10	1.40	3.30	72.39	72.20	70.10	69.40
LM23	53.50	54.00	52.00	52.50	80.50	83.50	85.00	89.50	65.15	66.25	63.75	69.45	5.95	6.50	1.90	3.50	84.41	84.80	69.60	77.20
LM29	52.50	52.50	51.00	49.50	78.50	67.00	83.50	90.00	64.55	61.65	52.15	62.55	5.15	4.85	0.90	2.80	75.90	74.60	61.40	60.60
LM45	54.50	52.50	51.50	51.00	77.00	82.50	82.00	90.00	59.55	57.85	62.85	61.75	5.40	5.70	2.20	3.60	90.40	89.20	75.70	78.20
LM85	52.50	53.00	50.00	50.50	76.00	80.00	80.50	90.50	61.90	58.80	63.00	63.25	4.30	6.30	1.30	2.30	75.70	80.80	68.60	66.30
Mean	49.00	48.50	50.50	47.00	75.50	78.50	84.00	85.50	58.10	58.70	60.55	63.60	7.55	5.90	2.00	3.40	69.10	69.30	65.20	65.70
LSD (5%)	3.14	2.69	2.95	2.29	4.56	6.15	4.68	4.84	7.01	7.08	6.97	9.16	2.16	2.43	0.82	1.34	9.87	10.49	10.73	11.71
SED	1.57	1.35	1.48	1.15	2.29	3.08	2.34	2.43	3.51	3.55	3.49	4.59	1.08	1.22	0.41	0.67	4.94	5.26	5.38	5.87
CV (%)	3.10	2.69	2.93	2.34	2.96	3.84	2.80	2.71	5.69	5.65	5.77	7.41	19.75	19.59	24.55	23.95	6.44	6.65	8.01	8.50

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM02XLM04	14.70	14.20	12.30	10.90	26.20	28.22	16.54	20.84	29.99	39.05	23.01	39.85	291.90	387.90	442.20	770.00	124.30	193.20	120.30	356.60
LM02XLM05	13.90	14.40	11.50	11.80	26.64	36.06	23.47	32.11	33.24	35.56	26.96	44.45	309.80	401.60	629.90	1198.00	154.30	204.50	245.50	578.90
LM02XLM09	13.00	14.70	10.00	13.20	23.47	24.39	13.59	26.62	27.49	37.50	35.06	40.30	276.80	364.20	429.50	1304.00	117.30	172.30	140.70	587.20
LM02XLM13	13.70	15.40	12.10	11.60	24.66	25.91	18.24	22.43	33.47	34.50	25.59	38.80	292.70	342.80	532.10	886.00	124.10	155.00	185.80	384.40
LM02XLM17	13.80	14.10	11.50	10.40	32.35	27.48	22.01	20.25	33.54	38.30	25.00	40.50	295.80	368.90	516.30	902.00	145.50	178.60	187.90	393.80
LM02XLM21	13.50	13.20	11.90	9.20	28.02	28.58	20.72	17.80	34.15	31.83	28.68	43.15	347.90	371.30	497.40	680.00	163.00	168.90	182.60	289.20
LM02XLM22	12.20	13.80	11.20	9.30	24.63	22.69	14.55	19.44	26.40	36.55	35.16	42.45	240.60	306.90	531.60	748.00	99.40	154.40	210.80	302.90
LM02XLM23	12.40	15.00	11.70	12.51	28.01	27.50	20.38	24.35	32.80	41.60	28.27	46.85	271.90	401.40	654.50	1264.00	124.20	224.10	234.80	578.20
LM02XLM29	14.90	14.90	9.90	10.82	26.40	25.71	21.67	20.34	34.25	38.10	28.69	44.20	227.50	397.10	438.70	1194.00	103.40	174.70	156.90	534.00
LM02XLM45	12.40	13.90	11.20	11.30	27.28	23.02	20.87	22.02	28.30	33.68	29.41	45.00	231.60	306.00	493.70	950.00	99.80	121.80	189.90	434.40
LM02XLM85	14.19	14.40	11.60	12.00	25.07	25.08	16.64	23.00	26.84	36.35	28.47	41.80	242.10	453.70	589.20	768.00	105.80	216.00	198.80	363.80
LM04XLM05	14.60	14.50	12.00	11.19	29.69	29.80	25.21	23.29	28.24	36.90	25.10	41.65	242.40	429.10	451.60	716.00	112.70	208.00	166.00	241.00
LM04XLM09	13.90	14.90	10.10	11.50	27.02	26.57	23.03	25.82	37.09	37.70	25.81	45.75	331.50	383.10	416.60	1165.00	154.30	188.40	126.10	559.00
LM04XLM13	14.20	14.50	13.10	11.71	29.78	27.22	20.03	23.46	35.40	31.98	27.59	44.75	332.20	330.90	565.00	818.00	145.60	147.90	174.20	358.40
LM04XLM17	13.60	14.20	11.40	11.31	24.84	25.65	20.04	23.65	31.23	38.80	25.49	45.44	260.70	468.00	485.50	943.00	117.00	229.90	190.40	408.90
LM04XLM21	14.70	16.50	12.30	12.40	18.51	27.98	20.05	27.50	49.33	38.95	27.62	43.05	278.50	371.60	572.20	903.00	127.00	177.90	212.10	429.10
LM04XLM22	15.90	14.90	12.60	12.80	23.61	26.53	20.38	27.48	31.57	33.75	24.82	43.90	269.60	284.00	567.40	923.00	114.60	138.10	166.10	411.90
LM04XLM23	15.50	17.80	10.20	13.91	31.11	32.21	14.20	31.97	25.20	35.80	30.90	35.70	322.00	466.50	460.30	1385.00	121.10	220.30	148.00	599.50
LM04XLM29	14.20	14.80	13.20	12.10	30.32	25.05	17.55	26.27	32.52	40.50	24.83	40.75	331.30	405.70	493.50	1058.00	143.20	186.30	139.20	510.90
LM04XLM45	13.90	15.40	11.30	12.11	25.66	27.85	21.72	24.94	37.28	34.35	26.71	51.00	279.50	293.10	450.50	1124.00	126.30	212.80	167.00	575.90
LM04XLM85	15.70	14.60	12.20	11.70	26.73	37.26	20.40	24.98	35.24	40.60	24.23	44.90	381.10	449.30	503.10	849.00	170.40	215.20	157.90	402.40
LM05XLM09	12.10	15.40	13.60	13.10	25.00	25.88	19.19	21.75	33.13	35.63	22.01	43.80	270.50	282.60	512.10	1312.00	110.80	128.80	134.60	548.70
LM05XLM13	14.20	15.90	12.00	12.81	31.78	28.65	15.85	26.97	29.49	34.55	31.25	45.95	276.80	472.10	526.80	1531.00	128.40	217.10	167.30	711.90
LM05XLM17	12.10	14.20	12.40	11.40	25.49	28.99	14.52	24.89	35.17	34.40	25.87	41.25	261.20	329.70	497.00	932.00	109.90	162.70	92.20	403.00
LM05XLM21	13.79	14.80	11.30	12.20	22.62	24.44	18.39	21.58	29.64	37.10	26.08	45.05	257.50	314.10	550.80	1037.00	116.10	155.10	195.70	431.00
LM05XLM22	15.30	14.60	10.90	13.51	22.30	30.68	13.90	23.85	31.75	28.95	27.29	44.65	255.90	456.00	428.80	1721.00	86.20	178.90	94.10	736.00
LM05XLM23	13.80	15.00	11.50	12.01	27.39	32.57	17.06	21.76	30.33	39.15	28.93	38.90	316.40	483.90	551.30	1140.00	126.70	228.20	183.30	515.90
LM05XLM29	14.60	14.50	12.20	12.53	28.80	32.12	18.78	33.44	34.43	33.60	23.03	34.25	309.70	330.50	384.30	1008.00	142.30	159.30	95.00	445.10
LM05XLM45	15.60	15.40	11.70	11.50	27.38	27.32	19.33	21.35	34.08	33.38	25.85	43.10	351.30	439.00	506.70	694.00	157.60	185.90	169.50	333.50
LM05XLM85	12.60	71.10	12.60	10.50	23.75	27.20	18.09	20.11	25.84	31.55	27.28	46.80	237.40	286.60	430.20	892.00	96.30	124.90	131.60	362.10
LM09XLM13	14.20	14.50	11.70	10.70	24.89	21.23	15.88	20.74	33.09	37.50	27.70	44.25	244.60	353.80	588.30	1135.00	98.00	151.50	172.30	441.30
LM09XLM17	13.70	14.10	12.50	12.30	23.11	27.47	17.92	25.90	28.89	35.20	23.59	42.65	252.40	384.20	569.60	1041.00	107.80	179.90	171.60	470.90
LM09XLM21	13.00	14.40	11.60	11.11	24.34	27.92	19.78	23.88	33.69	36.45	26.95	43.40	337.30	422.20	474.30	1015.00	139.40	214.50	154.80	440.20

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM09XLM22	12.80	14.10	11.80	11.90	21.26	27.59	17.19	24.72	33.68	37.75	22.39	45.95	249.00	471.50	565.50	1223.00	97.30	221.20	152.80	525.90
LM09XLM23	14.20	13.00	12.10	10.80	23.69	26.27	15.66	21.27	32.23	33.00	24.33	45.25	345.00	292.50	524.40	966.00	146.90	135.30	137.30	414.30
LM09XLM29	13.20	14.50	12.00	12.92	23.09	26.43	14.39	26.00	33.51	36.00	28.45	45.05	360.70	329.10	468.00	1026.00	156.30	156.50	130.80	434.10
LM09XLM45	13.30	14.60	12.10	11.82	24.44	25.72	17.76	19.02	34.40	36.25	29.55	43.65	307.40	347.50	571.20	775.00	150.40	167.80	201.00	306.00
LM09XLM85	13.89	14.20	12.50	11.52	24.49	26.35	16.64	13.87	31.71	36.60	28.08	43.55	337.60	354.20	537.40	824.00	140.20	161.80	167.90	174.00
LM13XLM17	13.80	13.70	12.30	11.70	21.60	26.09	16.84	25.41	27.53	33.40	25.83	41.65	199.50	425.40	567.00	959.00	79.80	195.90	196.80	451.20
LM13XLM21	14.00	14.20	11.60	12.30	25.01	24.47	19.94	22.20	26.54	35.35	26.35	42.95	264.60	413.40	535.10	860.00	117.00	199.80	212.30	369.60
LM13XLM22	14.10	17.40	12.50	11.81	17.08	26.11	19.51	22.71	28.35	30.45	26.63	43.65	292.70	470.20	544.70	958.00	82.70	212.70	209.00	461.60
LM13XLM23	14.50	14.90	12.90	13.80	25.73	27.68	18.02	25.85	32.95	37.59	23.49	45.05	394.10	389.50	569.60	1387.00	156.10	182.80	175.90	602.50
LM13XLM29	14.90	14.50	12.90	13.41	23.19	28.44	22.84	28.43	31.40	35.30	25.25	44.60	324.70	338.30	637.70	1205.00	137.10	197.50	196.00	552.10
LM13XLM45	15.00	16.60	12.20	13.10	23.96	26.57	19.27	23.90	29.95	38.10	31.53	48.10	333.60	467.50	604.20	1259.00	134.50	213.50	236.10	622.80
LM13XLM85	14.69	14.10	12.60	11.81	26.26	23.56	15.43	27.76	30.51	33.15	27.30	46.79	357.80	368.10	604.90	1056.00	155.10	155.90	191.30	492.10
LM17XLM21	13.01	14.30	11.15	11.41	24.26	25.45	14.58	23.37	27.00	32.07	28.07	37.55	285.90	264.00	404.70	1016.00	122.70	130.90	129.50	446.40
LM17XLM22	12.80	14.60	10.90	11.11	27.50	25.47	15.79	22.79	28.55	29.65	27.22	43.05	253.50	281.10	530.60	1008.00	123.50	133.60	183.20	445.60
LM17XLM23	13.09	13.50	9.80	11.00	23.75	24.78	14.49	19.58	24.94	31.75	29.09	43.00	215.90	317.60	407.90	789.00	96.10	146.40	138.20	319.60
LM17XLM29	13.40	14.20	11.90	13.11	27.58	26.46	18.50	27.47	29.83	36.40	26.97	42.25	212.20	395.00	474.70	1107.00	98.00	187.10	141.10	550.40
LM17XLM45	13.90	13.80	11.50	8.90	23.14	21.51	14.69	16.80	28.40	32.00	30.46	36.40	255.80	339.10	422.70	627.00	103.40	154.10	127.20	287.30
LM17XLM85	13.40	13.90	10.70	10.80	25.16	23.58	17.32	23.71	22.74	35.84	24.92	44.50	203.10	383.70	422.40	1117.00	85.80	190.00	135.30	573.10
LM21XLM22	14.00	15.70	12.80	10.10	25.63	23.81	14.83	27.92	27.99	31.75	26.00	42.50	292.20	311.90	522.50	821.00	121.20	133.90	134.00	360.40
LM21XLM23	13.20	14.90	11.50	11.20	25.31	24.52	16.07	21.03	30.14	35.90	28.99	44.75	303.70	432.90	546.60	754.00	133.60	187.50	184.50	290.10
LM21XLM29	14.20	15.20	12.60	11.11	26.83	29.81	18.11	22.78	33.40	32.10	24.81	44.95	328.20	353.30	561.60	1142.00	135.50	167.90	179.00	482.00
LM21XLM45	13.80	13.50	11.90	10.50	27.26	26.31	18.05	25.00	29.84	34.85	26.32	37.15	310.90	368.40	569.20	1009.00	144.70	183.00	180.90	471.10
LM21XLM85	12.60	15.50	12.10	10.51	25.40	25.92	17.53	21.82	30.99	40.85	29.75	42.40	285.70	425.50	520.40	750.00	125.80	219.90	184.10	277.20
LM22XLM23	13.90	15.40	12.10	11.80	28.03	32.01	20.62	25.34	34.75	36.93	25.34	41.85	421.50	460.50	451.50	1040.00	189.80	214.00	146.00	413.30
LM22XLM29	13.81	15.36	11.86	11.68	25.61	27.05	18.18	23.54	30.68	35.22	26.85	43.32	283.00	373.98	515.01	1028.99	121.92	175.06	165.38	453.67
LM22XLM45	14.50	13.10	12.30	12.00	18.63	22.51	13.10	22.62	28.15	30.15	30.14	42.00	251.90	313.90	491.30	1031.00	88.90	125.60	145.70	425.60
LM22XLM85	13.00	13.80	12.25	13.20	20.92	23.69	15.35	21.25	26.69	35.35	27.61	42.50	196.80	323.00	408.50	927.00	96.40	139.20	135.70	392.40
LM23XLM29	13.60	14.70	12.40	11.10	24.02	30.77	15.55	19.13	31.54	38.15	29.20	47.55	250.40	410.20	479.90	1040.00	110.30	188.30	161.50	327.40
LM23XLM45	13.90	14.20	11.40	11.60	26.53	32.88	15.64	26.33	32.90	34.15	26.33	44.20	346.40	321.10	554.80	1162.00	149.50	141.20	159.90	568.90
LM23XLM85	13.70	13.50	11.10	11.81	28.43	29.61	17.26	22.00	24.75	33.85	28.11	42.65	277.10	427.60	502.20	1069.00	114.40	182.40	188.80	443.20
LM29XLM45	13.50	14.60	12.20	11.30	27.96	27.27	15.36	24.84	27.34	31.65	29.10	45.55	214.00	322.80	512.10	754.00	95.50	149.60	151.10	316.70
LM29XLM85	13.60	15.20	11.20	12.61	24.98	28.86	24.01	22.37	30.85	31.78	28.73	42.80	269.30	310.40	447.90	1014.00	126.20	148.70	181.50	508.90
LM45XLM85	12.60	13.50	12.20	11.40	26.13	27.79	20.37	17.60	24.60	33.60	27.89	47.95	248.70	310.40	523.70	1164.00	110.60	142.90	187.70	506.40

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.1 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Parents	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**	**DS**	**NS**
LM02	13.20	14.40	11.40	11.62	27.27	31.47	16.24	24.03	32.11	40.50	28.81	44.25	287.00	417.40	454.50	1010.00	135.00	201.30	149.20	460.20
LM04	14.80	17.60	12.10	12.71	32.99	29.47	20.09	26.29	35.78	39.11	23.28	50.15	331.30	553.60	553.80	1327.00	149.50	268.40	163.20	672.90
LM05	15.20	15.40	12.80	12.60	23.85	28.46	21.22	20.67	29.20	34.73	25.95	46.40	229.10	373.00	556.10	1111.00	84.90	153.00	147.90	434.50
LM09	12.40	14.70	12.10	11.10	20.39	24.81	26.01	24.72	28.30	34.60	24.30	38.75	219.40	360.60	594.10	1138.00	94.50	156.00	161.20	465.30
LM13	14.91	15.20	13.50	11.50	27.21	26.53	23.82	25.71	29.10	32.21	23.27	40.65	285.40	297.90	641.20	1175.00	121.70	142.60	230.10	550.70
LM17	13.20	12.70	11.70	11.50	24.65	23.90	17.31	24.05	26.90	33.38	26.97	41.40	216.00	279.70	469.70	1147.00	100.50	128.70	173.70	575.80
LM21	12.71	14.50	12.20	10.51	27.79	28.74	16.16	15.39	30.65	39.55	24.20	47.75	330.00	436.30	543.20	670.00	154.60	224.70	157.80	232.40
LM22	13.30	13.50	12.60	11.40	23.98	26.27	21.33	25.39	26.19	25.73	23.78	35.05	278.80	286.90	569.80	902.00	116.10	121.20	156.30	354.70
LM23	14.00	14.50	11.70	10.60	27.18	27.00	19.73	22.16	30.60	40.63	24.88	48.40	281.70	395.00	579.00	1671.00	117.00	173.70	171.80	698.50
LM29	13.70	14.00	9.40	11.50	32.51	24.84	17.67	24.30	29.40	34.83	27.96	44.45	313.30	356.80	314.00	1171.00	132.40	159.60	98.80	561.50
LM45	15.40	15.00	12.10	10.70	23.98	28.01	15.59	22.82	30.00	37.45	24.80	44.45	277.70	419.70	561.70	1042.00	103.00	183.50	135.60	473.70
LM85	13.70	15.40	12.80	12.32	29.18	24.08	17.63	28.70	25.06	28.72	22.53	46.10	236.10	356.00	527.80	964.00	91.70	141.60	134.70	445.10
Mean	13.00	13.90	11.60	11.89	22.29	22.44	14.88	22.42	28.54	34.40	26.16	40.95	170.10	359.90	580.00	1088.00	70.50	158.40	174.50	509.00
LSD (5%)	2.23	18.19	2.07	2.43	6.31	8.01	8.36	8.66	8.14	5.35	8.33	7.85	119.70	123.90	192.20	563.00	55.88	64.77	85.91	309.90
SED	1.12	9.11	1.04	1.22	3.16	4.01	4.17	4.34	4.08	2.68	4.17	3.93	59.96	62.05	96.29	282.00	27.99	32.42	43.02	155.30
CV (%)	8.09	59.34	8.76	10.45	12.34	14.78	22.80	18.44	13.28	7.62	15.56	9.08	21.19	16.59	18.70	27.41	22.92	18.51	25.94	34.22

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.2 Specific combining ability effects of 66 F_3 families obtained from a 12x12 half-diallel cross tested under drought-stressed and non-stressed conditions in the field and greenhouse sites.

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Family	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM02 x LM04	-1.43	0.21	0.63	-0.64	-1.79	1.07	-1.90	-2.28	1.32	-2.99	0.11	-2.54	-0.55	0.50	0.15	-0.25	-1.03	-9.18	-2.08	-7.42
LM02 x LM05	-2.07	-1.54	-1.01	0.40	-1.83	-2.54	0.60	0.42	0.70	-1.74	0.74	5.67	-0.06	0.06	0.45	-0.72	-2.99	-0.32	-0.80	3.00
LM02 x LM09	-2.75	-1.72	-1.27	0.33	-4.08	-1.90	2.33	-1.04	0.93	-1.49	-8.05	2.47	0.20	0.98	-0.20	0.83	0.97	0.37	-5.50	11.08
LM02 x LM13	-2.71	-0.15	-0.52	-0.09	-2.15	-0.43	0.35	-2.53	0.86	-0.48	-0.36	1.85	0.09	-0.20	-0.09	-0.10	0.46	4.23	1.19	2.56
LM02 x LM17	0.21	2.14	1.43	0.75	1.49	4.03	0.09	-0.12	5.46	-0.50	3.54	0.98	0.95	0.08	-0.19	0.32	2.01	1.89	-1.03	-1.08
LM02 x LM21	-0.25	-1.04	-0.81	-0.48	0.39	-1.47	-0.03	3.46	-5.31	-3.75	0.71	-4.74	-0.45	-1.82	-0.38	0.27	3.72	-1.31	4.91	-6.46
LM02 x LM22	-1.04	-1.18	-1.86	-0.66	-2.76	-1.40	0.89	-0.81	-2.66	-1.59	-2.21	-8.71	-1.06	-0.06	-0.12	-0.67	0.09	-2.74	0.34	-11.27
LM02 x LM23	1.39	1.18	-0.04	0.03	0.60	0.82	0.04	-0.42	0.65	3.25	2.73	2.59	-0.81	1.00	0.16	-0.04	0.12	5.25	3.34	7.02
LM02 x LM29	2.11	0.68	1.00	-0.19	4.35	3.82	0.80	2.10	-1.70	3.14	-3.94	-2.06	1.19	-0.08	-0.06	0.20	5.34	4.28	-5.60	-4.19
LM02 x LM45	1.18	-0.57	-0.34	-0.70	1.35	-3.29	-1.83	-0.40	-0.39	1.97	-2.01	-0.47	0.26	-0.81	0.04	0.21	-9.03	-3.73	-2.68	2.14
LM02 x LM85	2.50	1.50	1.03	1.82	1.99	-0.65	-2.71	-0.52	-3.12	1.79	0.81	0.93	0.82	0.20	0.26	-0.40	0.54	-0.92	3.57	5.71
LM04 x LM05	-3.93	-4.57	-2.57	-2.02	-2.83	-1.93	2.81	0.82	-0.08	1.53	2.23	1.07	0.64	0.30	-0.33	-0.14	-1.70	-2.82	0.06	-3.72
LM04 x LM09	-1.11	-0.75	-0.05	-0.16	-1.08	-1.29	-1.16	0.71	0.77	1.34	-3.63	-1.38	0.25	0.41	-0.37	0.31	1.88	1.96	-4.00	1.47
LM04 x LM13	-2.07	-1.18	-1.41	-1.89	-0.15	-3.32	0.63	0.93	-3.09	0.84	1.42	-4.85	-0.46	-0.47	-0.27	-0.32	-4.14	-5.64	2.31	-3.95
LM04 x LM17	-0.14	-1.90	-0.64	-1.00	-0.51	-2.36	-2.02	1.44	2.67	3.67	2.80	1.18	0.44	0.17	0.28	0.20	-4.45	-2.95	0.61	-1.90
LM04 x LM21	-0.61	-0.57	-1.73	0.34	-0.61	0.14	1.80	-1.78	0.63	-3.98	-0.64	0.91	0.11	-0.53	0.19	0.05	-0.60	0.29	0.57	0.99
LM04 x LM22	-2.39	-1.72	-0.07	-1.09	-0.26	-1.79	1.43	0.36	-2.02	-1.86	0.60	-0.06	0.66	-1.33	0.48	-0.20	2.38	-0.78	-0.07	8.21
LM04 x LM23	3.54	5.64	1.77	4.34	2.10	6.93	0.21	-0.91	-0.33	0.12	-6.17	8.84	0.02	-0.27	-0.18	0.04	2.51	8.12	-0.44	8.10
LM04 x LM29	1.75	-0.36	1.01	1.81	0.35	1.43	0.47	2.48	0.78	0.41	-0.95	-4.11	-0.06	-0.95	0.54	0.68	5.45	4.69	3.30	-0.57
LM04 x LM45	-3.18	-3.11	-2.44	-2.18	-1.15	-3.18	-2.55	-1.33	-4.53	-2.16	-2.96	-0.02	-0.67	-1.48	-0.38	-0.11	-3.36	-1.70	-1.69	-2.50
LM04 x LM85	0.14	0.96	-0.75	-0.20	0.49	1.96	-0.70	-0.01	3.31	-0.29	-1.66	-3.37	0.21	-0.02	-0.36	-0.32	9.85	0.17	2.60	0.44
LM05 x LM09	-2.25	2.00	-0.89	-0.70	-2.11	-0.40	-4.08	-2.38	1.87	0.43	0.98	2.33	-0.29	0.07	0.06	-0.45	-2.66	5.95	8.47	3.61
LM05 x LM13	0.79	-0.43	-1.71	0.02	0.82	0.07	-1.32	-0.13	0.62	1.13	-0.85	-1.45	1.71	0.65	0.17	0.22	-1.89	5.30	-1.55	4.90
LM05 x LM17	0.21	-1.65	-1.72	0.25	1.96	-3.97	-0.43	-0.26	-1.72	4.32	-3.72	0.09	-0.34	-0.96	0.25	-0.27	-4.98	5.60	11.91	1.93
LM05 x LM21	-1.75	-1.82	-1.41	-0.78	-2.15	-4.47	0.05	1.08	-5.62	-0.19	-1.42	0.11	0.71	-0.17	0.51	-0.02	-2.68	-1.89	-5.35	1.51
LM05 x LM22	5.46	7.03	6.10	4.13	6.21	8.10	-0.51	3.16	0.01	-0.12	-0.46	5.39	-0.85	0.59	-0.53	0.74	6.00	0.72	-3.89	4.73
LM05 x LM23	-0.61	0.89	0.36	-0.97	-0.43	0.82	1.16	-2.43	-1.83	-2.33	1.36	-4.16	0.74	0.79	0.23	0.38	-6.40	-11.68	-6.50	-10.45
LM05 x LM29	-1.89	-2.11	-0.84	-1.10	-0.18	-0.18	-2.88	-0.09	0.15	0.20	-0.42	3.50	-0.68	0.11	-0.33	-0.29	3.57	-1.56	-2.51	0.22
LM05 x LM45	1.18	0.14	-0.39	-0.17	0.32	-0.79	0.46	0.25	0.77	4.69	-2.88	-9.42	0.56	0.03	-0.30	-1.07	6.78	1.06	0.73	-9.44
LM05 x LM85	-2.00	-2.29	-2.10	-1.14	-1.04	-3.65	0.94	-1.37	3.33	-1.65	-3.53	-2.26	-0.48	-0.40	-0.13	0.02	-5.27	-4.63	-2.61	-1.86
LM09 x LM13	4.61	-1.11	0.37	1.32	3.57	-0.79	0.49	1.50	-4.12	-0.76	0.71	0.85	0.08	-1.04	0.14	0.37	5.83	-4.67	-1.19	2.97
LM09 x LM17	-0.96	-0.82	-1.15	-1.54	0.21	0.18	-0.29	2.20	1.00	-2.03	1.98	0.59	-0.47	-0.61	0.12	-0.12	1.09	0.80	5.17	0.94
LM09 x LM21	-1.93	-2.00	-0.83	-0.41	-0.90	-1.32	-1.36	0.46	-2.12	0.72	2.65	-0.68	-0.71	0.49	-0.15	-0.07	3.35	-2.18	-1.83	-5.30

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), GH = greenhouse, DS = drought-stressed, NS = non-stressed

Appendix 3.2 continued

	DTH				DTM				PH				TN				SL			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Family	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM09 x LM22	0.29	-0.15	0.90	0.49	-0.04	3.25	0.01	0.89	1.61	4.59	4.69	5.59	-1.06	0.24	0.23	0.49	-0.63	2.86	0.10	4.29
LM09 x LM23	-0.29	0.71	-0.32	-1.81	-0.68	-1.04	-2.49	0.42	0.15	-3.68	-1.27	-9.70	0.22	-1.10	-0.25	-0.37	-0.01	-4.82	-3.58	-5.03
LM09 x LM29	0.43	-1.29	-1.29	-1.20	1.57	1.46	2.09	1.19	0.44	-2.79	0.03	-1.10	1.78	1.37	0.14	-0.44	0.13	0.11	1.10	0.15
LM09 x LM45	0.00	-1.04	-0.08	-1.07	2.07	-1.15	1.88	-0.10	4.82	2.44	-0.26	0.59	-0.25	-1.70	0.15	0.08	-5.74	-1.42	-4.94	-5.54
LM09 x LM85	0.82	1.53	2.87	0.36	3.21	1.50	1.53	0.37	-0.15	2.16	-0.17	-3.71	1.14	-0.19	0.07	-0.03	-0.48	-1.18	3.77	-6.69
LM13 x LM17	1.57	1.25	1.11	-0.21	0.64	1.64	0.89	1.48	-3.74	2.38	3.48	-0.44	-1.84	1.02	0.10	-0.65	1.00	-4.51	-3.50	-1.04
LM13 x LM21	-2.89	-0.43	-0.18	-1.45	-4.97	0.64	-0.87	-2.32	1.19	2.82	-2.00	-3.66	0.39	1.56	-0.21	-0.80	4.31	-2.08	-2.67	2.50
LM13 x LM22	-0.68	0.43	-2.54	-1.22	0.39	1.21	-0.62	-0.36	-5.27	2.64	-1.24	0.57	-0.65	0.72	0.05	-0.14	-7.64	0.39	-2.65	-8.06
LM13 x LM23	-0.75	-0.72	-0.53	1.38	-0.76	-2.07	1.05	0.48	7.02	1.88	-1.37	6.67	-0.35	-1.47	-0.07	0.90	4.11	2.02	-0.03	9.70
LM13 x LM29	0.96	0.78	1.29	0.95	-1.01	1.93	-0.86	0.21	2.11	-1.14	2.19	1.82	-0.48	0.00	0.14	-0.07	-1.45	-2.49	2.83	3.57
LM13 x LM45	-0.96	0.03	-0.08	-0.03	-0.51	2.32	1.36	-0.40	3.32	3.10	0.82	2.11	0.44	0.72	-0.38	0.15	2.71	8.18	3.90	8.31
LM13 x LM85	-1.14	-2.40	1.37	-0.92	0.14	-1.54	1.00	1.12	-0.19	-0.29	-2.28	0.46	0.49	0.23	0.37	0.14	1.52	-2.63	-4.24	-4.98
LM17 x LM21	0.54	0.85	0.91	0.03	0.17	1.10	2.13	-4.36	3.38	-1.94	-6.75	5.53	0.84	0.90	-0.29	0.52	-4.37	1.23	-3.48	3.66
LM17 x LM22	-0.75	-0.29	0.08	-0.94	-0.47	-0.82	-0.04	1.67	-0.80	-1.23	-1.73	-1.05	-0.36	-1.10	0.09	0.58	-3.10	0.04	0.22	-4.55
LM17 x LM23	-1.82	-2.93	0.27	-1.20	-3.11	-4.11	1.93	-1.06	-6.99	-1.14	-6.07	-3.29	-0.63	-0.39	-0.38	-0.49	-3.76	-7.16	-7.47	-6.82
LM17 x LM29	-0.11	-0.43	-0.40	1.15	-0.36	1.39	-1.49	-0.68	-6.02	3.55	2.23	1.21	-1.50	0.73	-0.27	-0.05	1.58	5.05	0.40	7.03
LM17 x LM45	-0.54	1.32	-0.31	0.71	-0.36	0.78	-0.15	1.61	-2.35	-0.42	0.87	-11.75	0.30	1.00	0.36	-0.84	5.87	2.88	-2.87	-10.09
LM17 x LM85	-1.21	-0.61	-0.70	-1.31	-3.22	-1.07	-1.85	-1.06	-1.13	-0.60	0.99	3.35	0.69	0.56	-0.13	0.25	2.60	1.85	0.77	3.06
LM21 x LM22	0.79	0.53	1.96	0.46	-0.58	-1.82	2.95	2.01	3.49	0.67	0.65	-1.62	-0.31	-0.85	-0.04	-0.37	2.23	8.39	-2.78	-1.11
LM21 x LM23	0.71	0.39	-0.09	0.03	1.28	0.39	-1.69	1.63	3.54	1.91	2.14	-5.31	-0.27	1.21	0.19	-0.54	-3.16	-3.15	1.48	-2.86
LM21 x LM29	-2.07	0.89	-0.80	-0.20	-0.47	1.89	-1.72	-1.01	0.50	-1.05	2.22	3.34	-0.85	-0.58	0.06	0.00	2.14	3.27	2.22	1.32
LM21 x LM45	1.50	0.64	0.44	0.86	1.53	1.28	-0.65	-2.50	-1.55	-1.87	2.29	3.17	-0.36	0.60	0.16	0.41	1.43	-1.69	1.00	1.48
LM21 x LM85	0.82	-0.79	-0.38	0.43	1.17	0.43	1.58	1.89	1.85	2.04	1.45	-2.57	-0.30	-0.69	0.01	-0.20	-0.74	5.67	1.17	-0.47
LM22 x LM29	-1.36	-0.75	-0.26	-1.97	-1.61	0.96	-0.63	-4.23	-2.90	-3.09	2.29	0.26	2.00	0.48	0.62	0.35	-3.41	-5.97	2.20	-0.99
LM22 x LM45	-2.29	-1.50	-0.59	0.60	-1.11	-2.65	0.18	-1.57	0.10	0.74	2.59	1.65	-0.21	0.45	0.13	-0.23	7.35	-4.91	-1.77	3.19
LM22 x LM85	-0.96	-1.43	-3.51	0.12	0.03	0.00	0.03	-2.04	-2.35	-2.64	-2.13	0.05	0.53	1.37	0.00	-0.24	-6.01	-4.12	-5.02	5.15
LM22x LM23	-1.07	-3.75	-0.66	-2.48	1.64	-0.54	-0.89	1.95	2.37	0.52	1.35	-0.49	0.42	-1.14	-0.49	-0.28	-0.32	4.53	2.13	-4.00
LM23 x LM29	-0.43	-1.40	-0.92	0.17	0.24	1.18	0.45	0.46	1.66	-0.75	1.95	-1.13	0.70	-0.91	-0.06	-0.31	0.42	2.81	7.19	4.38
LM23 x LM45	-1.36	-0.15	-0.21	-2.57	0.74	-0.43	0.52	-0.43	0.22	-3.67	-0.13	0.20	0.35	3.16	0.14	-0.10	0.52	2.93	1.99	-1.38
LM23 x LM85	-2.04	-2.07	0.49	-0.78	-3.61	-2.29	0.46	-1.70	-2.78	2.95	1.14	0.66	-0.80	0.08	0.42	-0.10	0.73	-1.56	-3.58	-1.56
LM29 x LM45	-1.14	-0.65	0.33	-0.02	-2.51	1.07	1.53	0.54	-1.17	0.52	2.47	1.31	-0.65	0.52	-0.05	-0.46	-9.15	-7.11	-0.32	-0.07
LM29 x LM85	0.18	-0.57	0.68	-0.94	0.64	1.71	4.10	0.16	1.54	1.93	-0.76	-3.39	-0.12	-0.31	-0.40	0.33	-3.56	2.17	-5.71	0.80
LM45 x LM85	-2.25	-1.32	0.10	-0.53	-2.36	0.10	-0.18	1.16	-1.77	-0.14	-1.57	3.95	0.02	-0.89	-0.20	0.25	-2.61	-4.27	5.23	1.78

DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height (cm), TN = tillering number, SL = spike length (mm), GH = greenhouse, DS = drought-stressed, NS = non-stressed

Appendix 3.2 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM02 x LM04	0.43	-1.11	1.01	-0.76	-2.13	-0.78	-3.61	-4.03	-3.97	-0.03	-5.84	-3.68	8.58	-48.30	-17.61	-204.43	-8.77	-24.83	-50.51	-106.16
LM02 x LM05	0.16	-3.72	-0.20	0.12	-0.36	6.51	4.42	8.82	2.24	-1.11	-0.78	1.99	51.98	19.34	100.75	145.07	37.99	21.61	73.29	117.79
LM02 x LM09	0.04	1.24	-1.28	1.82	-1.01	-1.92	-5.40	4.09	-3.84	-0.32	5.55	-2.37	33.70	7.79	-90.33	275.67	3.77	4.46	-30.55	150.61
LM02 x LM13	-0.33	1.45	-0.15	0.01	-1.70	-0.62	-1.18	-1.55	1.71	-1.72	0.50	-3.95	-15.41	-43.80	-41.96	-166.68	-5.04	-30.27	-19.06	-103.40
LM02 x LM17	0.78	0.36	0.26	-0.48	6.05	1.52	4.61	-2.30	4.92	2.12	-1.84	-0.75	67.02	10.48	14.08	-31.68	37.51	1.80	12.85	-47.72
LM02 x LM21	0.32	-0.54	0.28	-1.55	1.60	1.41	2.72	-3.84	1.68	-5.68	1.71	-0.12	30.19	-5.40	-41.28	-153.19	20.76	-16.99	-5.40	-70.14
LM02 x LM22	-1.19	0.79	-0.58	-2.05	0.38	-3.67	-2.97	-3.74	-3.73	2.30	7.73	1.11	-34.47	-49.09	-18.45	-225.57	-17.81	-5.00	30.58	-123.81
LM02 x LM23	-1.14	1.31	0.29	1.13	-0.31	-1.76	2.77	1.88	2.05	2.67	-0.08	3.10	-46.01	-0.39	98.44	143.98	-12.12	31.82	46.79	96.10
LM02 x LM29	1.34	1.33	-0.92	-0.76	-1.62	-1.86	2.68	-3.75	2.14	1.13	-0.07	1.62	-64.88	43.58	-38.90	171.52	-30.27	4.52	-8.75	64.44
LM02 x LM45	-1.35	0.47	0.52	0.33	1.22	-4.14	3.08	0.11	-2.44	-2.45	-2.81	1.09	-35.61	-47.39	7.70	23.65	-20.48	-41.69	10.06	0.44
LM02 x LM85	0.86	-3.83	-0.27	0.73	-1.73	-1.87	-2.27	0.82	-1.20	0.21	-0.14	-2.11	-36.93	83.49	60.23	-138.55	-15.70	43.15	16.18	-40.88
LM04 x LM05	-0.24	-4.85	-0.15	-1.19	1.63	-0.84	4.72	-2.72	-4.95	0.27	2.19	-2.79	-53.11	6.40	-41.12	-381.50	-16.08	7.07	21.33	-254.07
LM04 x LM09	-0.16	0.21	-1.25	-0.65	1.31	-0.95	2.58	0.77	2.43	-0.21	-0.80	1.69	13.60	-15.06	-72.57	91.77	15.06	-5.38	-25.01	88.42
LM04 x LM13	-0.93	-0.69	0.67	-0.74	2.83	-0.46	-0.83	-3.11	1.63	-4.40	1.51	0.73	14.86	-74.53	-19.56	-279.78	9.96	-51.34	-24.19	-163.41
LM04 x LM17	-0.52	0.03	-0.21	-0.38	-2.64	-1.44	1.20	-1.34	-0.39	2.39	-0.31	2.13	-13.42	57.35	25.06	-35.36	-4.20	27.40	34.61	-66.58
LM04 x LM21	0.42	2.18	0.06	0.95	-8.68	-0.28	0.58	3.46	13.03	0.91	2.99	-0.80	-60.45	-31.57	42.85	25.62	-23.90	-28.37	40.48	35.74
LM04 x LM22	1.41	0.63	0.21	0.59	-1.38	-0.94	1.94	1.52	-1.04	-0.62	0.21	0.71	0.25	-100.06	43.30	-94.71	0.43	-39.37	15.70	-48.75
LM04 x LM23	0.89	2.78	-0.83	1.79	2.79	1.94	-4.31	6.71	-8.27	-2.96	1.72	-9.14	-10.97	35.77	-55.62	221.26	-20.90	7.06	-21.51	83.40
LM04 x LM29	-0.46	0.01	1.12	-0.16	1.62	-3.64	-2.35	-0.30	-1.95	3.12	0.16	-3.05	41.33	-11.91	51.18	-9.39	13.45	-22.25	2.28	7.42
LM04 x LM45	-0.95	0.72	-0.29	0.38	-1.42	-0.33	2.48	0.80	2.80	-2.04	-0.86	5.39	-37.35	-101.77	-42.71	152.97	-8.68	21.53	4.87	107.96
LM04 x LM85	1.26	-3.43	-0.14	-0.37	-1.06	8.99	0.70	0.30	4.82	4.01	0.03	-0.71	93.47	46.90	-6.04	-102.61	42.86	24.87	-4.02	-36.25
LM05 x LM09	-1.42	-2.76	1.55	0.95	0.78	-2.08	-0.19	-1.28	1.04	0.19	-5.08	0.60	-15.47	-81.45	-20.91	161.06	-9.24	-37.02	-14.39	79.85
LM05 x LM13	-0.40	-2.80	-0.65	0.33	6.20	0.42	-3.94	1.42	-0.43	0.65	2.38	2.72	15.91	66.07	-11.32	355.01	19.65	35.11	-11.47	191.81
LM05 x LM17	-1.49	-2.75	0.45	-0.44	-0.08	1.36	-3.18	0.86	5.71	0.61	0.39	-0.07	42.54	-8.17	10.58	-123.90	12.58	10.38	-51.74	-70.89
LM05 x LM21	0.05	-3.69	-0.84	0.80	-3.10	-4.31	-0.56	-0.90	-1.86	1.85	-0.12	2.05	-31.11	-74.17	27.36	80.85	-9.58	-29.40	35.71	39.31
LM05 x LM22	1.35	-3.90	-0.69	1.32	-1.41	2.68	-4.18	-0.23	1.80	-2.70	-1.19	2.70	-0.05	95.18	-70.22	624.47	-19.61	20.27	-55.34	277.01
LM05 x LM23	-0.27	-3.51	-0.55	-0.21	0.49	1.84	-0.92	-1.81	-1.80	2.72	3.21	-4.87	10.40	49.25	62.11	-102.17	-2.28	28.34	36.20	1.49
LM05 x LM29	0.48	-3.81	0.03	0.12	1.40	2.90	-0.60	8.08	1.75	-1.15	-2.79	-8.84	18.28	-54.94	-53.87	-137.64	20.94	-15.93	-44.32	-56.73
LM05 x LM45	1.28	-2.07	-0.50	-0.31	1.68	-1.34	1.23	-1.69	3.23	-0.57	-1.91	-1.30	70.15	89.26	-32.99	-354.76	40.89	31.68	9.04	-132.78
LM05 x LM85	-1.30	48.80	0.16	-1.60	-2.63	-1.60	-0.51	-3.20	-2.12	-2.34	1.93	2.40	-38.53	-84.07	-74.73	-137.58	-18.67	-37.83	-18.50	-74.92
LM09 x LM13	0.38	-0.33	-0.63	-1.46	1.63	-3.77	-3.77	-3.73	1.89	2.59	2.34	0.71	-50.67	-14.84	-2.88	-16.43	-22.07	-17.05	-14.68	-54.22
LM09 x LM17	0.89	1.00	0.85	0.90	-0.39	3.06	0.29	3.23	-0.87	-0.02	-1.60	1.16	-6.60	35.16	80.48	8.78	-6.27	14.94	26.82	21.67
LM09 x LM21	0.03	0.58	-0.37	-0.06	0.80	2.39	2.04	2.34	0.50	-0.09	2.85	0.79	13.38	53.36	-54.87	83.72	-2.51	36.37	-5.35	73.13

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

Appendix 3.2 continued

	SPS				KPS				TKW				BI				GY			
	Field		GH		Field		GH		Field		GH		Field		GH		Field		GH	
Families	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
LM09 x LM22	-0.37	0.16	-0.52	0.10	-0.04	2.82	-0.66	1.56	2.23	4.47	-3.17	3.93	-34.60	116.70	40.77	151.13	-15.77	59.25	7.38	91.44
LM09 x LM23	0.91	-0.80	0.20	-1.03	-0.92	-1.24	-2.27	-1.67	-0.31	-4.33	-1.17	1.20	17.11	-79.54	-24.24	-252.14	12.01	-33.07	-22.03	-75.56
LM09 x LM29	-0.15	0.85	0.50	0.84	-1.83	0.44	-4.35	1.59	1.40	0.14	2.06	2.08	98.90	-13.41	-3.09	-94.97	38.12	-0.80	-3.99	-43.13
LM09 x LM45	-0.24	1.12	0.22	0.40	1.50	0.32	0.29	-3.08	2.48	1.16	3.35	-0.22	26.46	4.04	27.11	-249.55	27.62	13.99	42.36	-135.77
LM09 x LM85	0.78	-3.42	0.23	-0.32	0.57	0.78	-2.01	-8.62	2.36	1.25	0.61	-0.70	55.26	-9.64	14.18	-181.04	19.74	-2.87	12.52	-238.46
LM13 x LM17	-0.08	-0.62	0.01	-0.03	-3.46	1.39	-1.21	1.47	-2.13	0.01	-0.38	-0.92	-74.36	49.33	57.45	-97.70	-34.34	19.42	16.59	-49.31
LM13 x LM21	-0.04	-0.23	-0.86	0.83	0.28	-1.18	1.22	-0.94	-4.93	0.17	-0.24	-0.45	-33.28	21.94	-57.14	-95.47	-12.54	7.65	6.83	-48.70
LM13 x LM22	-0.15	3.69	0.12	-0.40	-5.90	1.05	1.25	-2.32	-0.50	-1.16	-2.03	1.21	31.20	117.06	-25.24	-137.92	-19.76	55.57	18.17	-24.05
LM13 x LM23	0.14	0.48	0.53	1.62	-0.68	-0.10	-0.31	1.38	2.82	1.59	-1.43	0.51	55.37	-14.46	-16.43	144.24	18.08	-4.47	-20.07	61.42
LM13 x LM29	0.48	0.24	0.55	1.07	-3.23	2.18	3.70	2.69	0.22	0.80	-0.82	1.05	21.46	-26.91	87.32	60.18	9.80	26.43	17.09	23.60
LM13 x LM45	0.39	1.78	-0.33	1.30	-0.93	0.90	0.80	0.39	-0.56	4.71	5.33	3.96	32.02	102.02	9.38	209.66	10.46	47.47	35.65	129.85
LM13 x LM85	0.50	-4.05	-0.16	-0.44	0.70	-2.28	-3.07	3.67	2.32	-0.41	3.55	1.49	64.32	-18.45	31.36	26.69	33.53	-17.00	-3.28	28.43
LM17 x LM21	-0.03	1.00	-0.51	0.79	-0.75	0.24	-2.07	1.72	-2.71	-2.71	0.27	-4.35	15.47	-72.10	-109.79	179.32	-0.43	-31.92	-41.87	74.33
LM17 x LM22	-0.44	2.00	-0.81	-0.22	4.72	1.05	-0.23	-0.62	1.07	-1.79	0.88	2.60	23.72	-37.44	14.76	30.98	28.47	-8.99	26.24	6.15
LM17 x LM23	-0.26	-0.59	-0.96	-0.26	-2.45	-2.43	-1.80	-3.59	-2.46	-3.80	0.23	0.80	-43.93	-49.00	-84.52	-334.22	-15.31	-25.31	-25.93	-175.26
LM17 x LM29	-0.01	1.75	0.17	1.56	1.05	0.82	1.44	3.33	-0.62	1.99	2.10	1.32	-44.25	73.30	8.73	81.40	-15.41	33.08	1.04	68.12
LM17 x LM45	0.30	0.76	0.45	-2.07	-1.86	-3.38	-2.26	-5.44	0.06	-1.06	2.21	-6.48	-1.85	18.13	-46.85	-303.25	-8.49	-0.35	-30.26	-159.41
LM17 x LM85	0.21	-3.27	-0.87	-0.53	-0.16	-1.67	0.33	0.94	-2.50	2.22	-2.58	1.62	9.72	37.15	-34.89	206.56	-4.34	27.31	-18.68	155.72
LM21 x LM22	0.60	1.57	0.63	-0.91	2.53	-1.75	-1.98	5.41	-1.98	-1.06	2.14	0.77	-1.00	-49.67	-3.73	-55.36	-1.92	-33.82	-29.33	3.13
LM21 x LM23	-0.31	0.00	0.34	0.05	-0.78	-3.84	-0.89	-0.95	-0.62	-1.21	-0.17	0.88	-2.89	35.23	15.40	-269.35	-1.32	-2.41	4.49	-122.54
LM21 x LM29	0.63	1.16	0.66	-0.37	0.05	3.00	0.37	-0.21	0.53	-3.69	-1.25	1.31	15.85	2.22	42.00	216.08	-5.32	-1.73	15.82	81.96
LM21 x LM45	0.04	-0.43	0.11	-0.13	2.53	0.08	1.01	4.05	-0.99	-0.49	-2.93	-6.71	36.87	-5.43	55.51	179.54	21.48	-1.40	7.58	106.62
LM21 x LM85	-0.75	-2.38	0.20	-0.56	0.03	-0.47	-0.13	0.16	2.32	5.90	3.42	-1.74	27.47	52.97	23.03	-60.08	7.88	46.67	14.69	-57.98
LM22 x LM29	-0.77	-0.11	0.32	-0.04	-2.00	-3.68	-2.38	-2.70	-0.76	2.23	-1.85	-1.05	-87.82	17.38	103.11	22.32	-35.86	5.95	30.99	41.62
LM22 x LM45	0.53	-0.75	0.11	0.63	-4.09	-2.92	-3.53	-0.13	-1.06	-1.56	1.91	-0.16	-15.17	-55.05	-19.54	60.75	-20.00	-39.50	-15.42	-6.24
LM22 x LM85	-0.55	-4.16	0.49	1.52	-2.67	-1.99	-1.27	-2.01	0.47	3.84	0.53	-0.32	-70.87	-31.52	-76.93	-23.67	-10.21	-18.50	-19.46	-10.12
LM22x LM23	0.18	1.29	0.20	-0.05	3.79	4.39	4.12	1.35	5.46	3.12	-1.18	-0.95	129.48	62.92	-68.72	-122.88	70.51	38.99	-17.09	-66.69
LM23 x LM29	-0.29	0.75	0.70	-0.91	-3.62	2.01	-1.80	-5.30	1.72	1.27	1.81	3.80	-32.67	-4.01	-0.09	-172.09	-12.36	-2.49	13.01	-195.46
LM23 x LM45	-0.19	0.41	-0.47	0.23	0.43	4.71	-1.01	4.22	2.93	-1.66	0.03	-0.73	26.05	-47.74	6.30	46.47	14.26	-24.64	-11.15	81.68
LM23 x LM85	0.03	-4.37	-0.29	0.00	1.55	1.09	0.01	-0.21	-3.44	-2.08	1.63	-2.19	-38.92	32.09	2.48	-27.07	-19.64	1.68	23.36	-14.76
LM29 x LM45	-0.64	0.11	0.30	-0.24	1.81	0.63	-1.54	1.24	-3.09	-2.84	2.19	1.64	-60.07	-28.29	8.89	-265.13	-23.18	-15.59	0.61	-157.94
LM29 x LM85	-0.12	-2.54	-0.61	0.53	-2.18	2.01	5.94	-1.24	2.39	-2.67	0.98	-2.00	3.28	-46.27	-15.79	15.06	12.10	-13.34	34.53	63.54
LM45 x LM85	-1.32	-4.90	-0.04	0.00	1.17	1.58	2.99	-3.93	-3.78	-0.13	0.81	3.05	-30.66	-55.76	-3.36	260.81	-8.48	-23.69	20.48	96.55

SPS = spikelets per spike, KPS = kernels per spike, TKW = thousand kernel weight (g), BI = fresh biomass (g/m^2), GY = grain yield (g/m^2), CV% = coefficient of variation, SE = standard error, LSD = least significant difference, NS = non-stressed, DS = drought-stressed

CHAPTER 4

Correlation and Path Coefficient Analyses of Yield and Yield Components in Drought Tolerant Bread Wheat Populations

Abstract

Correlation and path coefficient analyses of economic traits is a key guide to selection of promising genotypes in plant breeding programs. The aim of this study was to determine the degree of association between yield and yield-components of drought tolerant wheat populations using correlation and path analyses. Twelve selected parents and 66 of their F_3 families were evaluated both under drought-stressed and non-stressed treatments in the field and greenhouse conditions. Experiments were conducted using a 13 x 6 alpha-lattice design with two replications. The following data were collected: number of days to heading (DTH), number days to maturity (DTM), plant height (PH), productive tiller number (TN), plant height (PH), spike length (SL), spikelets per spike (SPS), kernels per spike (KPS), thousand kernel weight (TKW), fresh biomass (BI) and grain yield (GY). Significant correlations ($P<0.05$) were observed between GY with PH, TN, SL, KPS, TKW under both drought-stressed and non-stressed conditions. Partitioning of correlation coefficients into direct and indirect effects revealed high positive direct effects of KPS and BI on GY under drought-stressed conditions. Among all the assessed traits, BI had significant simple correlations of 0.75 and 0.90, and high direct effects of 0.76 and 0.98 with GY under drought-stressed and non-stressed conditions, in that order. The top performing genotypes, LM02 x LM05, LM02 x LM23 and LM13 x LM45, showed high mean values for KPS, TKW and BI. The overall association analyses indicated that the latter three traits had significant influence on GY performance and are useful for selection of drought tolerant breeding populations of wheat.

Key words: *correlation coefficient, drought stress, drought tolerance, path coefficient, wheat*

4.1 Introduction

Wheat (*Triticum aestivum* L., 2n=6x=42, AABBDD) is one of the commodity crops of the world being the major source of food and industrial products (Okay et al., 2014). Wheat surpasses maize and rice in cultivation area and production levels and is therefore the most important cereal crop (Dababat et al., 2015). This status can be attributed to its versatility in providing a vast range of food products and its higher nutrition content when compared to other cereals (Curtis, 2002). As a result of rising population growth and economic development, global wheat demand is steadily increasing (Röder et al., 2014). Notably, the demand for wheat in the developing world is expected to increase by 60% by the year 2050, driven by urbanisation and changing consumer preferences (Manickavelu et al., 2012).

Yield and production levels are stabilising in major producing countries in Asia and Europe (Mills et al., 2018). However, various countries in Africa annually imports a significant amount of wheat to offset local demand (Gianessi 2014). Yields of wheat vary across different environments, with higher yields reaching 8 to 10 t/ha achieved in temperate regions which present the most favourable environment for wheat production (Röder et al., 2014). Nevertheless, the mean productivity of wheat in Africa is below 3 t/ha (Negassa et al., 2013).

Winter wheat requires cool and moist growing conditions during vegetative growth and increasing temperatures towards the end of the growing season (Asseng et al., 2011). Hence, according to Curtis (2002), the most important requirement for optimum wheat production is the availability of enough moisture during the crop's life cycle. Therefore, unavailability of adequate soil water due to drought stress at any growth stage in wheat will lead to poor crop development and yield loss.

Drought stress remains an important yield limiting abiotic factor in semi-arid regions around the world. Under dryland wheat production systems, drought stress is the main cause of yield loss leading to complete crop failure under harsh conditions (Farshadfar et al., 2011). According to Rolli et al. (2015), the incidence of drought will increase in the future due to the impact of global warming and this will lead to more depressed yields in previously productive regions. It is therefore important to find strategies that will improve wheat productivity under drought conditions to ensure sustainable global food supply (Nawaz et al., 2015). To reduce the impact of drought stress, breeding of superior cultivars that can perform well under varying moisture deficit levels can lead to better yields in tropical and sub-tropical regions (Okuyama et al., 2004).

The main objective in any breeding program is to improve grain yield, a polygenic trait that is determined by a wide range of physiological and biochemical processes (Shukla et al., 2015).

Being quantitative traits, both grain yield and drought tolerance are subject to genotype (G) x environment (E) interaction limiting identification and selection of superior genotypes (Farshadfar et al., 2013; Shi et al., 2017). Therefore, information on the association of yield and yield components in wheat under drought conditions is important to improve selection efficiency for high yields and drought tolerance (Shimelis, 2006). According to Gurmu et al. (2018), correlations of agronomic traits can be used to identify traits with high heritability that can be used to simplify selection of complex traits such as yield. Therefore, selection towards highly correlated agronomic traits can enhance genetic gains under drought-stressed and non-stressed conditions.

Simple correlation analysis shows the degree of association between yield components but does not reveal the direct influence of yield components on grain yield. Yield components often have inter-relationships and indirect effects on each other which confound their final contribution to grain yield (Mashilo et al., 2016). As a result, simple correlation analysis alone is insufficient to explain the contribution of individual traits on grain yield. Path coefficient analysis is a standardised partial regression coefficient that partitions correlation coefficients into direct and indirect effects revealing the causal-effect relationship among yield components (Bello et al., 2010). It is a reliable statistical technique that helps quantify the inter-relationship between yield components and determine their contribution to grain yield (Gurmu et al., 2018). This is essential in identifying economic traits that contribute the most to grain yield and to prioritize traits for selection. Therefore, the aim of the study was to assess the association between yield and yield components in wheat and identify the most important components to improve grain yield and drought tolerance.

4.2 Materials and methods

4.2.1 Plant materials

Twelve bread wheat parental lines and their 66 F_3 families derived from targeted crosses using a half-diallel mating design were evaluated in this study. The details of parents and their crosses were presented in Chapter 2, Section 2.2.1.

4.2.2 Study sites

The study was conducted during the 2017/2018 growing season in two sites as summarised below:

4.2.2.1 Field and greenhouse experiments

The genotypes were evaluated under field conditions at Ukulinga Research Farm, while a greenhouse trial was carried out at the University of KwaZulu-Natal, Pietermaritzburg campus using a 13 x 6 lattice square design. Details of experimental conditions are described in Chapter 2, Section 2.2.2.

4.2.3 Data collection

Data on 10 agronomic traits were collected under both the field and greenhouse experiments. Details of data collection and measurements are presented in Chapter 2, Section 2.2.3.

4.2.4 Data analysis

A combined analysis of variance (ANOVA) was performed on the assessed agronomic traits using Genstat 18th Edition (VSN International, 2015). Mean comparison was done using Fisher's least significance difference (LSD's) at 5% level of significance. Pearson's correlation coefficients (r) were calculated using SPSS (SPSS, 2012), to determine the magnitude of the relationship among agronomic traits according to Miller et al (1958). The correlations were calculated separately for drought-stressed and non-stressed conditions. Path coefficient analysis was conducted and used to partition correlation coefficients into direct and indirect effects on grain yield according to Dewey and Lu (1959) using Microsoft Excel 2016.

4.3 Results

4.3.1 Pearson's correlation coefficients

Correlation coefficients (r) describing the degree of associations between grain yield and yield-components under drought-stressed (below diagonal) and non-stressed (above diagonal) are summarised in Table 4.1. Significant positive correlations ($P<0.05$) were observed between GY and PH (r = 0.334), TN (r = 0.476), SL (r = 0.257), KPS (r = 0.377), TKW (r = 0.378) and BI (r = 0.754) under drought stressed conditions. Under non-stressed conditions, GY had significant positive correlations ($P<0.05$) with all the traits except SPS. In the study the highest correlation values were observed between GY with BI (0.904), PH (0.532) and SL (0.526). BI was significantly and positively correlated with all the traits except KPS and TKW under drought stress and SPS under non-stressed conditions. Significant positive correlations were also observed between DTH and DTM, SL and KPS as well as DTM and TKW under both drought-stressed and non-stressed conditions.

Table 4.1 Correlation coefficients of nine agronomic traits with grain yield in 12 parental lines and 66 F_3 families under drought-stressed (below diagonal) and non-stressed (above diagonal) conditions.

					Non-stressed						
	Traits	**DTH**	**DTM**	**PH**	**TN**	**SL**	**SPS**	**KPS**	**TKW**	**BI**	**GY**
Drought-stressed	**DTH**	1	0.634**	0.360**	0.247	0.369	0.051	0.273*	0.088	0.567**	0.398**
	DTM	0.664**	1	0.242*	0.152	0.250*	0.056	0.313**	0.231*	0.390**	0.234*
	PH	-0.073	0.160	1	0.277*	0.395**	0.044	0.381**	0.186	0.655**	0.532**
	TN	0.277*	0.274*	0.181	1	0.129	-0.025	0.008	0.011	0.438**	0.378**
	SL	0.145	0.035	-0.022	0.336**	1	0.022	0.402**	0.495**	0.495**	0.526**
	SPS	0.327**	0.228*	-0.014	0.455**	0.532**	1	0.052	0.048	0.033	0.007
	KPS	0.147	0.131	-0.143	0.199	0.267*	0.145	1	-0.004	0.415**	0.467**
	TKW	-0.048	0.329**	0.108	0.057	0.179	-0.034	-0.024	1	0.311**	0.329**
	BI	0.238*	0.235*	0.307**	0.636**	0.413**	0.500**	0.181	0.214	1	0.904**
	GY	-0.115	0.168	0.334**	0.476**	0.257*	0.184	0.377**	0.378**	0.754**	1

* $P < 0.05$; ** $P < 0.01$; DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length, SPS = spikelets per spike, TKW = thousand kernel weight, BI = fresh biomass, KPS = kernels per spike, GY = grain yield

4.3.2 Path coefficient analysis under drought stressed condition

The path coefficients analysis for nine agronomic traits on grain yield under drought stress are presented in Table 4.2. Among the measured agronomic traits, the highest direct effects on grain yield were observed for BI (0.764) followed by KPS (0.309) under drought stressed conditions. DTM, PH, TN and TKW also showed positive direct effects on GY under the same condition. Negative direct effects on GY were observed for DTH (-0.423) and SPS (-0.141). Further, negative direct effects of SL (-0.054) on GY were recorded though statistically non-significant. High positive indirect effects were recorded for BI through all the other traits. DTH had indirect effects of -0.117 and -0.101 on GY which can be selected through TN and BI, respectively.

Table 4.2 Direct (bold face values) and indirect effects of nine agronomic traits on grain yield of 12 parental lines and 66 F_3 families under drought-stressed conditions.

Traits	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	BI	Correlation with GY
DTH	**-0.423**	0.13	-0.004	0.016	-0.008	-0.046	0.045	-0.006	0.182	-0.115
DTM	-0.281	**0.195**	0.009	0.016	-0.002	-0.032	0.04	0.044	0.180	0.168
PH	0.031	0.031	**0.054**	0.010	0.001	0.002	-0.044	0.014	0.235	0.334**
TN	-0.117	0.054	0.010	**0.057**	-0.018	-0.064	0.062	0.008	0.486	0.476**
SL	-0.061	0.007	-0.001	0.019	**-0.054**	-0.075	0.083	0.024	0.316	0.257*
SPS	-0.138	0.045	-0.001	0.026	-0.028	**-0.141**	0.045	-0.005	0.382	0.184
KPS	-0.062	0.025	-0.008	0.011	-0.014	-0.02	**0.309**	-0.003	0.138	0.377**
TKW	0.02	0.064	0.006	0.003	-0.010	0.005	-0.008	**0.133**	0.164	0.378**
BI	-0.101	0.046	0.017	0.036	-0.022	-0.071	0.056	0.028	**0.764**	0.754**

* P < 0.05; ** P< 0.01; DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length, SPS = spikelets per spike, TKW = thousand kernel weight, BI = fresh biomass, KPS = kernels per spike, GY = grain yield

4.3.3 Path coefficient analysis under non-stressed condition

The path coefficient analysis for nine agronomic traits on grain yield under non-stressed condition are presented in Table 4.3. The highest positive direct effects on GY under non-stressed conditions were observed for BI (0.976). Other traits that exerted positive direct effects on GY were TN, SL, KPS and TKW. Traits including DTH (-0.101), DTM (-0.133), PH (-0.147) and SPS (-0.018) had negative direct effects on GY. Further, the results showed positive indirect effects for BI through all the other traits on GY.

Table 4.3 Direct (bold face) and indirect effects of nine agronomic traits on grain yield of 12 parental lines and 66 F_3 families under non-stressed conditions.

	DTH	DTM	PH	TN	SL	SPS	KPS	TKW	BI	Correlation to GY
DTH	**-0.101**	-0.084	-0.053	0.006	0.030	-0.001	0.042	0.005	0.553	0.398**
DTM	-0.064	**-0.133**	-0.036	0.004	0.021	-0.001	0.049	0.014	0.380	0.234*
PH	-0.036	-0.032	**-0.147**	0.007	0.033	-0.001	0.059	0.011	0.639	0.532**
TN	-0.025	-0.020	-0.041	**0.024**	0.011	0.000	0.001	0.001	0.427	0.378**
SL	-0.037	-0.033	-0.058	0.003	**0.082**	0.000	0.062	0.024	0.483	0.526**
SPS	-0.005	-0.007	-0.007	-0.001	0.002	**-0.018**	0.008	0.003	0.032	0.007
KPS	-0.028	-0.041	-0.056	0.000	0.033	-0.001	**0.155**	0.000	0.405	0.467**
TKW	-0.009	-0.031	-0.027	0.000	0.033	-0.001	-0.001	**0.061**	0.303	0.329**
BI	-0.057	-0.052	-0.096	0.010	0.041	-0.001	0.064	0.019	**0.976**	0.904**

* P < 0.05; ** P< 0.01; DTH = days to 50% heading, DTM = days to 50% maturity, PH = plant height, TN = productive tiller number, SL = spike length, SPS = spikelets per spike, TKW = thousand kernel weight, BI = fresh biomass, KPS = kernels per spike, GY = grain yield

4.4 Discussion

Drought stress reduces performance of wheat genotypes and is a major contributor to declining productivity of wheat around the world (Curtis and Halford, 2014). Breeding for improved yield and drought tolerant wheat genotypes is one of the main goals for breeders aiming to release cultivars for tropical and sub-tropical regions.

In this study under drought stress, GY had high positive correlations with PH, TN, SL, KPS, TKW and BI signifying the importance of these traits in improvement of grain yield in water limited environments. Families LM02 x LM21, LM02 x LM23 and LM13 x LM85 scored high for these traits and were found amongst the top 15 performing genotypes under drought stressed conditions. Similar results have been reported by Ahmadizadeh et al. (2011), del Pozo et al. (2016) and Mwadzingeni et al. (2016) who reported positive correlations among the above-mentioned traits with grain yield under drought-stressed conditions. Among these, BI showed a very high positive correlation (0.75) with GY suggesting its value for selection for grain yield. This could be the reason why all the top ten genotypes had high biomass values under drought stress. It was also observed that DTH, DTM, PH, TN, SL and SPS highly correlated with BI which indicate their usefulness in improving this trait. Therefore, an increase in the stated traits could lead to enhanced vegetative growth which translates to higher plant biomass production (Demura and Ye, 2010). This increases the area of the plant available for photosynthesis and enhances production of photo-assimilates required for grain filling. Under non-stressed conditions, GY had positive correlations with all the traits except for SPS. This indicates that an increase in the performance of all these traits could lead to an improvement in GY. Notably, PH had a high positive correlation ($r > 0.50$) with yield under non-stressed conditions indicating its importance in moisture optimum or irrigated growing conditions. This agrees with Mwadzingeni et al. (2016) who stated that tall and late maturing genotypes have more time for photo-assimilate production under non-stress growing conditions than shorter and early maturing genotypes leading to higher grain yield performance. This was reflected by the families LM04 x LM23, LM05 x LM13 and LM05 x LM22 which had high DTM and PH values and were among the highest yielding genotypes under non-stressed conditions (Table 2.4). SL also showed high positive correlations with yield under non-stressed conditions. SL is considered amongst the major determinates of final grain yield as it contributes directly to kernel dry matter (Sharma et al., 2003). The authors further stated that it has advantages over other yield components in increasing yield because the spike stays green longer than other plant parts allowing for extended photosynthesis and is located higher on the plant thus utilizing available sunlight more efficiently. Strong positive correlations were also observed between DTH and DTM under both drought-stressed and non-stressed conditions. This could be because DTM is directly dependent on and can only occur after DTH. Therefore, delayed heading will directly lead to delayed maturity and vice versa.

The traits that had high correlations with GY under drought stress can be used to improve drought tolerance in the selected genotypes. Yet, path coefficient analysis is useful in partitioning correlation coefficients into direct and indirect effects which reveal the actual contribution of yield components on GY (Akram et al., 2016). This helps in identifying the primary traits that have a direct influence on GY which could further be used simultaneously to increase selection efficiency. Among the traits, TN, KPS, TKW and BI had a positive direct effect on GY under both drought-stressed and non-stressed conditions. Among these traits, BI had the strongest direct effect on yield under drought-stressed (0.764) and non-stressed conditions (0.976). This indicates that BI had the greatest contribution and influence on the final GY. This trait could be important for indirect selection for grain yield under drought-stressed and non-stressed conditions. Richards et al. (2014) suggested that plant breeders should focus on traits that improve plant biomass to increase grain yield under dryland conditions. This also agrees with Saleem (2003) who observed high biomass values in better performing wheat genotypes under drought and non-stressed conditions. Positive direct effects of KPS and TKW on GY under both test conditions were expected as an increase in kernel number and weight will directly increase grain yield. These results agree with Qin et al. (2015), who attributed the increase in grain yield of wheat in China to the increase of kernel number and weight. However, there was a negative correlation between KPS and TKW under drought-stressed conditions. Similar results have been reported by Wu et al. (2012) under drought-stressed conditions and Dabi et al. (2016) under non-stressed conditions. This suggests that simultaneous increase of KPS and TKW may be difficult to achieve due to compensations between the two traits arising from competition of available assimilates or complex regulation of plant physiology (Slafer et al., 2014). This is more pronounced under drought-stressed conditions as the amount of photo-assimilates produced are less when compared to plants grown under optimum moisture conditions as observed for families LM04 x LM21 and LM13 x LM45 (Table 2.4). The positive direct effect of TN indicates its contribution to better yields, because more tillers are associated with a good crop stand and more spikes (Jamro and Rashid, 2017). Therefore, improvement of TN will lead to better yield under both drought-stressed and non-stressed conditions. DTH had negative direct effects on GY whereas DTM had positive direct effects on GY indicating that a reduction in DTH and an increase in DTM under drought conditions could lead to an increase in grain yield. This is because a combination of early heading and late maturity in a genotype extends the grain filling duration. Increasing the grain filling duration is essential in improving yield under drought stress as it extends the time for starch accumulation which increases kernel size and final yield (Altenbach et al., 2003; Semenov et al., 2009). Under drought-stressed condition, PH showed positive direct effect on GY but negative direct effects under non-stressed condition. This shows the importance of extending the PH under stress because drought shortens the internodes as well as reduces the number of nodes in wheat (Ahmed et al., 2007). However, under non-stressed conditions, excessively tall plants are susceptible to lodging and direct loss of yield due to pre-harvest sprouting of lodged plants on moist soils.

In this study, path coefficient analysis was useful in partitioning correlation coefficients providing useful information for selection by revealing the direct and indirect effects of yield components on GY. For instance, yield components such as PH and TN were highly correlated with GY under drought stress but had a small direct influence on GY. Therefore, the above-mentioned traits will not be effective in improving grain yield despite the observed high correlations. Notably, under drought stressed conditions, SL and SPS had high correlations with yield but showed a negative direct effect on GY. Similar results were observed for DTH, DTM, PH and SPS under non-stressed conditions. Variable results between simple correlation and path coefficients in some traits in wheat have been reported by Khan et al. (2010), Anwar et al. (2009) and Kashif and Khaliq (2004).

Path coefficient analysis revealed that BI was the most important trait for indirect selection of GY as it showed high correlations with GY accompanied by high positive direct effects in both drought-stressed and non-stressed conditions. Furthermore, BI had high positive indirect effects on GY through all the measured traits in both drought-stressed and non-stressed conditions. This information shows the utility of path coefficient analysis in identifying key traits that influence grain yield.

4.5 Conclusions

Correlation and path coefficient analysis is useful in identifying traits that are related and contribute to GY. They also help to understand the inter-relationship between yield components and GY. This allows for more efficient selection of better performing genotypes for yield and drought tolerance. Correlation and path analysis revealed that BI is the most important trait contributing to grain yield under both drought-stressed and non-stressed conditions. Furthermore, DTH, DTM, PH, TN and SL had significant positive correlations with BI. KPS and TKW also showed strong significant correlations and direct effects on GY under drought stress indicating the importance of these traits when selecting wheat genotypes for drought stress. It was also observed that delayed maturity in combination with early heading could also be targeted to improve GY under drought-stress. This study identified KPS, TKW and BI as the major yield components that can be used to select for drought tolerance. This was observed on better performing families namely, LM02 x LM05, LM02 x LM23 and LM13 x LM45 which had high values for these traits under both drought-stressed and non-stressed conditions. These traits, as revealed by both simple correlation and path coefficient analyses can be used effectively to improve selection efficiency and genetic gains for drought tolerance in wheat.

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Overview of Research Findings and Implications of the Study

Dryland wheat production in South Africa is affected by recurrent drought associated with climate change. The known wheat cultivars grown in the country are susceptible to drought stress. In the past there was no dedicated breeding program geared towards developing wheat cultivars with tolerance to drought. Developing drought tolerant wheat cultivars is a major goal for the Agricultural Research Council-Small Grains Institute (ARC-SGI) to improve wheat productivity in dryland agro-ecologies of South Africa. In an attempt to use a well-characterised germplasm pool in its pre-breeding program, the ARC-SGI imported drought tolerant wheat germplasm from the International Maize and Wheat Improvement Centre (CIMMYT). A study by Mwadzingeni et al. (2016) screened 96 drought tolerant wheat genotypes and selected 12 lines with superior yield performance under drought-stressed and non-stressed conditions. These lines were crossed in a half diallel mating design to produce 66 families that were advanced to the F_2 generation (Mwadzingeni et al., 2018). The families needed to be advanced to the F_3 generation and evaluated for early generation selection for genetic advanement of high perfoming families. Identifying key traits that enhance drought tolerance by conducting association studies is key for selection gains. This chapter summarises major research findings and recommendations for early generation selection of F_3 wheat families for genetic advancement.

The specific objectives of the study were:

i. to undertake early generation selection of wheat genotypes for drought tolerance and agronomic traits for genetic advancement.
ii. to determine the combining ability effects and the mode of gene action that controls yield and yield components in selected wheat genotypes under drought-stressed and non-stressed conditions.
iii. to assess the association between yield and yield components in wheat and identify the most important components to improve grain yield and drought tolerance.

Early Generation Selection of Wheat Genotypes for Drought Tolerance and Agronomic Traits

Seventy-eight genotypes consisting of 12 parents and their 66 F_3 families were evaluated in two contrasting water regimes under greenhouse and field conditions in the 2017/2018 growing season. The following agronomic traits were assessed: number of 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), fresh biomass (BI) and grain yield (GY). Analysis of variance, variance components, heritability and genetic advance were calculated. The main findings are as follows:

- Highly significant differences ($P<0.05$) were observed for DTH, DTM, PH, TN, KPS and TKW among the genotypes under the two water regimes.
- Variance components and heritability estimates among agronomic traits and yield showed high values for days to heading and fresh biomass under drought stress.
- Drought incidence reduced mean yield of wheat genotypes by 54.73% compared with non-stressed environments.
- The F_3 families LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 were relatively high yielding in both stressed and non-stressed conditions and selected for genetic advancement.

Combining Ability Analysis for Yield and Agronomic Traits among F_3 lines of Wheat under Drought-stressed and Non-stressed Conditions

The above data set were used to calculate the combined and individual site analysis of variance. Estimates of general and specific combining ability of individual traits were calculated in two contrasting water regimes under greenhouse and field conditions in the 2017/2018 growing season. The core findings of this study are as follows:

- LM17 had negative general combining ability (GCA) effects for DTH, DTM and PH which are desirable traits for drought escape and tolerance.
- Parental lines LM02, LM13 and LM23 had high positive GCA effects for GY and can be utilised to improve grain yield under drought-stressed conditions.
- The F_3 families such as LM02 x LM05 and LM02 x LM17 consistently yielded the best across both drought-stressed and non-stressed conditions and are recommended for further genetic advancement.

Correlation and Path Coefficient Analyses of Yield and Yield-components in Drought Tolerant Bread Wheat Populations

The following agronomic data: DTH, DTM, PH, TN, SL, SPS, KPS, TKW, BI and GY were subjected to correlation and path coefficient analyses. This was aimed to pinpoint key agronomic traits for further selection under drought-stressed and non-stressed conditions. The main findings were as follows:

- Significant positive correlations ($P<0.05$) were observed between GY and PH, TN, SL, KPS, TKW and BI under drought-stressed conditions

- BI had high significant simple correlations of 0.75 and 0.90, and high direct effects of 0.76 and 0.98 with grain yield under drought-stressed and non-stressed conditions, in that order.
- The high yielding genotypes such as LM02 x LM05, LM02 x LM23 and LM13 x LM45, had high mean values for KPS, TKW and BI indicating their importance in selection for drought tolerance.

Implications of findings of this study for future drought tolerance breeding in wheat

- High yielding families including LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45 should be advanced to the F_4 generation using the single seed descent selection method.
- Double haploid techniques should be used to instantaneously fix the homozygosity of the selected families (LM02 x LM05, LM13 x LM45, LM02 x LM23 and LM09 x LM45) to reduce breeding cycles and for enhanced variety release.
- Parental lines LM02, LM13 and LM23, that had good general combining ability for grain yield under drought stress and can be used to generate breeding populations and selection of ideal transgressive segregates for improved yield and drought tolerance.
- High heritability and genetic advance values for DTH and BI signifies their importance for direct selection to improve drought tolerance in bread wheat.

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