BREEDING MAIZE (*ZEA MAYS* L.) HYBRIDS WITH COMBINED TOLERANCE TO *STRIGA HERMONTHICA* AND LOW SOIL NITROGEN FOR THE NORTHERN SAVANNA ZONES OF GHANA

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BY

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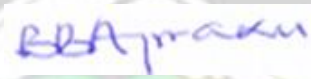
DECLARATION

I, declare that except for references to other people's work which have been duly acknowledged, this dissertation is my own work and that, to the best of my knowledge, no part of it has been presented for the award of any degree or diploma at Kwame Nkrumah University of Science and Technology (KNUST), Kumasi or elsewhere.



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ABSTRACT

Maize is an important staple crop widely produced and consumed in West and Central Africa (WCA). Low soil nitrogen (low-N), recurrent drought and *Striga hermonthica* infestation are major constraints to maize production and productivity in WCA. The specific objectives of this study were to (i) determine genetic diversity among 100 selected set of maize inbred lines using Simple Sequence Repeat (SSR) and Single Nucleotide Polymorphism (SNP) markers (ii) classify the selected set of inbred lines into heterotic groups using the general combining ability effect of multiple traits (HGCAMT) method, SSR and SNP markers, and to compare effectiveness of the different methods in grouping the inbred lines, (iii) determine the combining ability and heterosis for grain yield and agronomic traits of the selected set of inbred lines under *Striga* infestation, low-N and optimal growing conditions, (iv) determine the grain yield potential and yield stability of hybrids derived from the selected inbred lines under *Striga* infestation, low-N and optimal growing conditions.

Substantial genetic and phenotypic variability existed among the inbred lines used in this study for grain yield, *Striga* resistance/tolerance and low-N tolerance. Although SSR markers used in this study were highly informative, the use of large number of SNP markers made the SNP comparable with the SSR for genetic diversity analysis, and better than SSR in cluster and population structure analyses. Genetic analysis of 150 hybrids derived from the North Carolina Mating Design II revealed significant differences among the hybrids for grain yield, *Striga* resistance and low-N tolerance. General combining ability and SCA mean squares were significant for grain yield and most traits under optimal, *Striga*-infested and low-N environments and across environments, indicating that both additive and non-additive gene actions were

important in the inheritance of the traits. The inheritance of grain yield under low-N and across environments were controlled largely by additive gene action, while the inheritance of grain yield under optimal and *Striga*-infested environments were controlled largely by non-additive gene action. Non-additive gene action largely modulated the inheritance of almost all traits measured under *Striga*-infested environments, except for *Striga* damage syndrome rating at 8 WAP. The SNP genetic distance based heterotic grouping method was identified as the most efficient in grouping the inbred lines into heterotic groups.

The yield response and stability analyses of the 150 hybrids and six local checks over 10 contrasting environments indicated that 62% of the hybrids had average stability across environments, while 8% had above average stability and were adapted specifically to either *Striga*-infested or low-N environments. The hybrids TZdEI 215 x TZdEI 192, TZEI 378 x TZdEI 215 and TZEI 3A x TZdEI 192 were the highest yielding and most stable across environments. They are recommended for further testing and commercialization in the savanna zones of Ghana and other countries in WCA.

DEDICATION

I dedicate this dissertation to the families of Mr. Bright Kofi Adu and Mr. Isaac Kofi Owusu for their invaluable support throughout this study. To my beloved husband Mr. Godfred Owusu, thank you for always motivating me to reach for the stars.

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"Psalm 9:1, I will praise thee, O Lord, with my whole heart; I will shew forth all thy marvelous works."

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LIST OF ABBREVIATIONS

AATF	The African Agricultural Technology Foundation
AFLP	Amplified Fragment Length Polymorphism
ANOVA	Analysis of Variance
ASI	Anthesis-Silking Interval
BPH	Better-Parent Heterosis
CIMMYT	International Centre for Maize and Wheat Improvement
CSIR	Council for Scientific and Industrial Research
DA	Days to Anthesis
DAP	Days after Planting
DMBQ	Dimethoxy-P-Benzoquinone
DNA	Deoxyribonucleic Acid
DYSK	Days to Silking
EASP	Ear Aspect

EH	Ear Height
EHARV	Ears per plot
EPP	Number of Ears per Plant
FAO	Food and Agriculture Organization
FAOSTAT	Statistical databases and data-sets of the Food and Agriculture Organization of the United Nations
FWT	Field weight
GCA	General Combining Ability
GD	Genetic Distance
GEI	Genotype x Environment Interaction
GGE	Genotype Main Effect plus Genotype x Environment Interaction
GT	Genotype by Trait
GYLD	Grain yield
HC	Husk cover
HGCAMT	High General Combining Ability of Multiple Traits
HSGCA	Heterotic Group's Specific Combining Ability and General Combining Ability of Grain Yield
IITA	International Institute of Tropical Agriculture
LD	leaf death score
Low N	Low Soil Nitrogen
MET	Multi-Environment Trials
MI	Multiple Trait Base Index
MIP	Maize Improvement Program
MoFA	Ministry of Food and Agriculture
MPH	Mid-Parent Heterosis

NUE	Nitrogen Use Efficiency
PASP	Plant Aspect
PC	Principal Components
PCA	Principal Component Analysis
PIC	Polymorphic Information Content
PHT	Plant Height
PS	Plant stand
PHARV	Plants per plot
PROC GLM	General Linear Model Procedure
QPM	Quality Protein Maize
QTL	Quantitative trait locus
RAPD	Randomly Amplified Polymorphic DNA
REML	Restricted Maximum Likelihood
RFLP	Restriction Fragment Length Polymorphism
RL	Root Lodging
S.E	Standard Error
SARI	Savanna Agricultural Research Institute
SAS	Statistical Analysis System
SCA	Specific Combining Ability
SL	Stalk Lodging
SNP	Single Nucleotide Polymorphism
SRID	Statistics Research and Information Division
SSA	Sub-Saharan Africa
SSR	Simple Sequence Repeats
STRCO1	*Striga* emergence count 1
STRCO2	*Striga* emergence count 2
STRRAT1	*Striga* damage syndrome rating 1
STRRAT2	*Striga* damage syndrome rating 2

WAP Weeks After Planting

WECAMAN West and Central Africa Collaborative Maize Research Network

CHAPTER ONE

1.0 GENERAL INTRODUCTION

Maize (*Zea mays* L.) is the third largest planted crop in the world after rice and wheat and the second most traded cereal after wheat (FAOSTAT, 2014). Globally, growth in production of maize is about 2.2% per annum, mainly through harvested area increase of 0.9% per annum and global average yield increase of 1.5% per annum (Fischer *et al*., 2014). Annual average yield in sub-Saharan Africa (SSA) is 1.81 MT per ha, representing about one-third of the world's average yield (FAOSTAT, 2013). Yield improvement in SSA is determined largely by the limited access of small-scale farmers to yield-enhancing inputs such as improved seeds, fertilizers, machinery, and irrigation technologies (Banziger and de Meyer 2002). Even where improved varieties are available, the adoption has been poor due to the failure of new varieties to address farmers' preferences or needs and their growing conditions (Banziger and Diallo, 2002). Often improved varieties selected for high yield under optimal agronomic conditions, when grown by farmers in marginal production areas have failed to provide sufficiently large advantage to be adopted (Cleveland and Soleri, 2002).

Maize is an important staple crop for human consumption in SSA, providing at least 30 percent of the food calories for more than 50% of the population in SSA.Thus, its availability and affordability have been central to food security (Badu-Apraku and Fakorede, 2017) of countries in the sub-continent (CGIAR, 2016). It is projected that if maize yield in SSA could be increased from the current 20% to 80% of the potential yield, then, SSA would attain self-sufficiency in 2050 (van Ittersum *et al.,* 2016). Yield

potential is location and year specific and highly controlled by temperature, solar radiation, water, nutrient supply, pest and diseases (Van Wart *et al*, 2013.). Therefore, difference between yield potential and actual farm yield of a cultivar can only be achieved if the environmental factors are perfectly managed to enhance genetic potential of the cultivar. The three key production constraints responsible for yield reduction in SSA are soil nutrient constraints (44% of losses), weeds (19%) including *Striga* sp., and drought (18%) (Gibbon *et al*. (2007). The problem of poor soil fertility, particularly low-N could be alleviated by the addition of inorganic fertilizer as commonly done in high input agricultural systems in developed countries. However, fertilizer supply is limited and the cost is prohibitive for SSA farmers (Mosier *et al.*, 2005). As a result of high fertilizer costs, application rates in SSA are the lowest in the world, (Kidane *et al*., 2006). The high cost of fertilizer calls for the need to maximize nitrogen use efficiency (NUE) of maize varieties (Wong and Nortcliff, 1995), and encourage the use of nitrogen use efficient varieties along with modest fertilizer use and other integrated soil fertility management practices to stabilize yields and increase the productivity of maize in SSA. Low soil fertility is also closely associated with *Striga hermonthica* infestation (Ransom *et al.*, 1990).

Striga hermonthica (Del.) Benth is an obligate parasitic weed commonly found in cereals in the savannas of West Africa and in the mid altitudes of East Africa. It causes yield losses of between 20-100% in maize (Mohamed *et al*., 2001; Fischer *et al*, 2014). *Striga* control methods commonly used in SSA include hand weeding, host plant resistance; chemical control and intercropping with catch or trap crops. The use of host plant resistance is considered the most preferred because it is sustainable, affordable and more environmentally friendly for resource poor farmers (Mahmoud *et al*, 2013; Badu-Apraku *et al.*, 2004). The integration of *Striga* resistant maize varieties into *Striga*

management programs offers the most effective and sustainable control measure for the parasitic weed (Yoder and Scholes, 2010). Maize production in Africa takes place mainly in rainfed systems. Maize yield is highly correlated with rainfall, which is important because drought is a defining feature of rainfed production environment.

About 40 % of Africa's maize-growing area faces occasional drought stress, resulting in yield losses of 10–25 %. About 25 % of maize crop suffers from frequent drought, with losses of up to half the harvest (Fisher *et al*., 2015; CIMMYT, 2013). Drought stress also hinders nutrient uptake. Maize grain yield is reduced by up to 80% under combined drought and low-N conditions (Betrán *et al.*, 1997; Bänziger *et al.*, 1997). Although the effects of uncertain and highly variable rainfall can be mitigated through the use of irrigation, SSA has the lowest level of irrigation development in the world. Only 4% of agricultural land in SSA is irrigated. Maize yields in Ghana are very low, averaging 1.74 t ha^{-1} compared to an achievable yield of 6 t ha^{-1} (SRID, 2013). The Guinea savanna agro-ecologies of Ghana, representing the Northern, Upper East and Upper West regions of Ghana have the greatest potential for increased maize production because solar radiation is high and incidence of pests and diseases is very low in these regions. However, maize productivity in northern Ghana is greatly constrained by drought, low soil fertility, and *Striga* infestation (Badu-Apraku *et al.*, 2003; BaduApraku and Fakorede, 2017). Under field conditions, there are also often complex interactions among these stresses with more devastating effects on yield of maize (Cechin and Press, 1994; Kim and Adetimirin, 1997). This implies that for the highest productivity of maize in the savanna zones each variety grown must be able to withstand a wide range of drought stress, nitrogen availability and *Striga* infestation, a need that justifies the development and deployment of multiple stress tolerant varieties (Badu-Apraku and Fakorede, 2017) in the northern savanna zones of Ghana. Substantial progress in breeding stress tolerant maize for African farmers has been

achieved. Since 1990, the International Maize and Wheat Improvement Center (CIMMYT) and the International Institute of Tropical Agriculture (IITA) together with their global network of partners have developed several maize varieties (including, breeding populations, open- pollinated varieties, hybrids, and inbred lines) and relevant breeding techniques, aimed at addressing major production constraints. These include drought, low nitrogen and acid soil conditions, *Striga* and insects (Edmeades *et al.*, 1997; Manyong *et al*.,
2000).

The present study focused on the utilization of new inbred lines developed by the West and Central Africa Collaborative Maize Research Network / International Institute of Tropical Agriculture (WECAMAN/IITA), for development of locally adapted maize hybrids with multiple-stress tolerance/resistance to *Striga* and low-N for the savanna zones of Ghana in particular and West and Central Africa (WCA) in general. Before hybrid development, there is a need to have adequate knowledge of the level of genetic diversity within the selected inbred lines for grain yield and other Striga and low-N adaptive traits as well as the brreding value of the inbred lines to guide the selection of prospective parents of the desired hybrids. Since majority of the inbred lines selected for this study are newly developed, there is little to no information on them with regards to these mportant genetic parameters, which would facilitate their use in hybrid development. To address these research gaps, the following specific objectives were considered in this study:

i. Determine genetic diversity of a set of 100 early maturing white and yellow endosperm inbred lines using Simple Sequence Repeat (SSR) and Single Nucleotide Polymorphism (SNP) markers,

ii. Classify the set of inbred lines into heterotic groups using different methods of grouping, iii. Determine the combining ability and heterosis for grain yield and agronomic traits of the set of inbred lines under *Striga* infestation, low-N and optimal growing onditions, iv. Determine grain yield potential and stability of hybrids derived from the inbred lines under *Striga* infestation, low-N and optimal growing conditions.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Production and productivity of maize in sub-Saharan Africa

World maize production is estimated at 872 million tons, planted on over 177 million hectares. African production represents 7.9% of the world production. Trends in maize production in Africa point towards a steady growth, mostly due to the increase of cultivated area and the use of improved maize varieties (Manyong *et al.,* 2000). The largest African producer is South Africa with nearly 12 million tons, followed by Nigeria with about 9.5 million tons (FAOSTAT, 2014). In Ghana, the annual production of maize in 2016 was 1.72 million tons and was cultivated on 8.65 million hectares of land (SRID, 2017). Comparison of the average production of maize yields in metric tons for the periods 2010-2012 and 2013-2015 showed a decline in production of about 1.71% (SRID, 2016). A report by World Grain forcasted that maize production in SSA in 2018-2019 will decline by 5% of 72.2 million tons produced in 2017 as a result of devastating effects of Fall Armyworm and reduction in maize area in South Africa (Lyddon, 2018).

Maize yields (1.81 t ha^{-1}) obtain in SSA is one of the lowest in the world (FAOSTAT, 2013). Generally, yield improvements in most SSA countries follow a period of stagnant to sluggish yield increase in the 1980s and 1990s (Nin-Pratt *et al.,* 2012)). From 1991 to 2014, countries like Ethiopia (86 kg/ha/yr) and Mali (60 kg/ha/yr) have relatively higher yield increases and hold promise for attaining 80% of their yield potentials by 2050 (van Ittersum *et al.,* 2016). By 2050 the world's population will reach 9.1 billion with the greatest population increase expected to occur in developing countries (Delacy *et al.,* 1996; Dayanandan *et al*., 1998; Badu-Apraku *et al.,* 2011a). By 2050 the global demand for food, feed and fiber is expected to grow by 70 percent

compared with demands in 2007, while, increasingly, food crops may be used for bioenergy and other industrial purposes (FAO, 2009). In order for Africa to feed its growing population without greater reliance on imports and/or major expansion of agricultural area, it is generally agreed that greater investment in research in both public and private sectors is needed to accelerate agricultural intensification through yield growth, crop intensification, and increased irrigated area (World Bank, 2009; 2013 and Pardey *et al*., 2013), and improved extension services (Edye and Laina, 2016).

2.2 Maize production constraints

2.2.1 Low access to improved seeds

Seeds are first and foremost, the source of most food, at least of plant origin, and therefore have the greatest socioeconomic benefit to human welfare of any known biological device (Tahirou *et al*., 2009). Louwaars and Marrewijk (1999) indicated that, the development and use of high yielding seed varieties have been the technological force behind the successful green revolution, the accessibility of food at prices lucrative for farmers and affordable by the general public, and a reduction in rural poverty. Thus, seed provision, both in normal and disaster years, is a prerequisite for increasing food production, improving farmers' incomes, alleviating poverty, and ensuring food security. Maize production has become a lucrative activity since the demand for maize from the feed industry, small livestock producers and local consumers has increased markedly in sub-Saharan Africa. An understanding of factors currently limiting production and deployment of improved maize seeds in sub-Saharan Africa is of paramount importance in promoting maize production, improving farmers' income, alleviating poverty, and ensuring food security (Tahirou *et al*., 2009). Van

Amstel *et al*. (1996) acknowledged that the factors contributing to food insecurity in sub-Saharan Africa include insufficiencies in the supply and delivery of farm inputs, in which suitable, reliable, and sustainable seed systems play a significant role.

2.2.2 Effects of nitrogen deficiency on the growth and yield of maize

Nitrogen (N) plays a vital role in nutritional and physiological status of plants, promotes changes in mineral composition of plant, and is the most important element for plant growth and development (Karasu, 2012). The optimal amounts of plant nutrients in the soil cannot be utilized efficiently if nitrogen is deficient in plants. Variations in nitrogen (N) availability affect growth and development of maize (Zea mays L.) and may lead to changes in crop physiological conditions at flowering and in kernel set (Uhart *et al.*, 1995). Uhart *et al.* (1995) evaluated the effects of different levels of N availability on crop development, crop radiation interception, radiation use efficiency, and dry matter partitioning in a commercial maize hybrid (DK636) under field conditions in Argentina. The authors found that nitrogen deficiency slightly reduced leaf emergence rate, and strongly diminished leaf expansion rate and leaf area duration. Nitrogen deficiencies reduced radiation interception as much as radiation use efficiency and their effects on the ear dry matter/total dry matter ratio at harvest were associated with crop growth rate reductions at flowering. Dry matter partitioning to reproductive sinks at flowering and the ear dry matter/total dry matter ratio at harvest were also reduced by N shortages (Uhart *et al.*, 1995). In other studies also nitrogen deficiency decreased photosynthetic activities in maize leaves (Baszyński *et al*. 1975), and also decreased grain yield and plant weight in old and improved maize hybrids (Ding *et al*., 2005). Li *et al*. (2012) studied the effects of nitrogen on the photosynthetic characteristics of a stay green inbred line (Q319) and a non-stay green inbred line (HZ4) and found that nitrogen fertilization has significant effects on promoting the net photosynthetic rate in leaves at the grain-filling

stage and on single-plant grain yield at the harvest stage in the stay green inbred line, whereas there is no significant effect in the non-stay green inbred line.

Nitrogen deficiency or excess can result in reduced maize yields. However, the amount of optimum nitrogen fertilizer varies among cultivars and agro-ecological conditions (Sezer and Yanbeyi, 1997). African farmers understand the benefits of proper fertilization, but many factors prevent widespread use. In fact, African farmers use less than 10% of the world average amount of fertilizer. The principal constraints of SSA maize yields are low soil fertility and low use of chemical fertilizers. It is established that SSA displays a combination of high soil nutrient deficits and very low fertilizer use that comes from a set of failures on input and output markets. On the demand side, poor price incentives, highly seasonal and variable production due to increasing rainfall variability, lack of liquidity, credit or insurance and lack of knowledge about fertilizers undermine farmers' capacity to adopt the technology or to reap the benefits of its use (Druilhe and Barreiro-Hurlé, 2012). At the Abuja Declaration on "Fertilizer for the African Green Revolution" in 2006, African Union Member States agreed to increase fertilizer use to 50 kg ha^{-1} by 2015. However, average fertilizer use remains between 5 and 10 kg ha^{-1} in most countries in sub-Saharan Africa (FAOSTAT, 2015).

2.2.3 *Striga* and maize plant

2.2.3.1 Economic importance of *Striga in maize production*

Modern agriculture is threaten by parasitic plants, a case of pathogenenis more pronounce between species of relatively close evolutionary ancestry. Although, parasitic plants may have the ability to parasite a wild range of crop species, some species are most preferred and thus, severe outbreaks are mostly limited to certain hostpathogen combinations (Nweze *et al.,* 2015). The origin of *Striga hermonthica* is unclear and may have originated in north-east Asia (Scholes and Press, 2008). It is the

largest and most destructive of the *Striga* species and considered as one of the most serious weeds in Africa (Oswald, 2005). The damage *Striga* causes is major and the harvest losses are obvious (De Groote *et al*., 2007). The damage varies between fields and areas. Some fields may experience just a small yield loss while others suffer a yield loss of up to 100% (Berner *et al*., 1995). After S*triga* has spread to a field, the damage it causes increases every season if nothing is done to combat it (Khan *et al*., 2006). As it is a major problem for farmers in Africa, several methods have been developed to combat *Striga*; the problem is that the economic effect of these methods is hard to evaluate and therefore it is challenging to decide which one will be the economically most favourable for the farmers (Andersson and Halvarsson, 2011). *Striga* slows down the growth of the host in two ways: it damages its photosynthesis and uses its nutrients, causing a deficit (Khan *et al*., 2006).

Striga' is the Latin word for 'witch'. Witchweed, Yan maemod (Thai), Buta (Kiswahili) and other common names for *Striga* often refer to the word 'witch', presumably because plants diseased by *Striga* display stunted growth and an overall drought-like phenotype long before *Striga* plants appear (Spallek *et al*., 2013). The genus *Striga* comprises about 30 obligate root-parasitic plants that occur naturally in parts of Africa, Asia, and Australia (Sauerborn *et al*., 2007). Most *Striga* species parasitize grass species (*Poaceae*) with *S. hermonthica*, *S. asiatica S. aspera*, *S. forbesii* and *S. gesnerioides* causing immense losses to major staple crops like cowpea (*Vigna unguiculata*), finger millet (*Eleusine corocana*), maize (*Zea mays*), pearl millet (*Pennisetum glaucum*), rice (*Oryza sativa*), sugarcane (*Saccharum officinarum*) and sorghum (*Sorghum bicolor*) in SSA (Scholes & Press, 2008; Spallek *et al*., 2013). *Striga gesnerioides* (Willd.). Vatke is the only *Striga* species that is virulent to dicots (Mohamed and Musselman, 2008).

2.2.3.2 Origin and life cycle of *Striga*

Striga possibly originated from a region between the Semien Mountains of Ethiopia and the Nubian Hills of Sudan (Atera and Itoh, 2011). This region is also the birthplace of domesticated sorghum (*Sorghum bicolor* L.), which is a major host species for several *Striga* species, including *S. hermonthica* (Delile) Benth. and *S. asiatica* (L.) Kuntze, and is believed to be the host on which monocot-parasitizing *Striga* species have evolved and spread throughout Africa and Asia (Vasudeva-Rao and Musselman, 1987; Nweze *et al.,* 2015). *Striga* species are annual plants and most of the life cycle occurs underground (Spallek *et al*., 2013). The genus *Striga* is classified as a monophyletic group belonging to the family Orobanchaceae Vent (Bennett and Mathews, 2006; Nweze *et al.,* 2015). *Striga* normally emerges about 4-7 weeks after planting and after another 4 weeks it develops purple flowers. The *Striga* flower produces about 50,000 – 500,000 seeds per flower (Berner *et al*., 1995). It causes most damage to its host before it emerges out of the soil and therefore, the use of postemergent herbicides is not of great value. If the seedlings do not germinate, they can stay dormant in the soil for over 20 years (De Groote *et al*., 2007). Growth of dormant seeds in the soil are stimulated to germinate by exudates from roots of host plants (Parker *et al*., 1977).

Ejeta *et al*. (1997) noted that, numerous *Striga* plants may penetrate and attach to a single individual host plant by an organ known as haustorium. This infection structure attaches to host roots and penetrates and establishes vascular connections with them (Hood *et al*., 1997). Spallek *et al*. (2013) indicated that, parasitic plants have evolved specific traits which allow parasitism or reflect the consequences of adaptation to a parasitic life style (Nweze *et al.,* 2015). Critical stages in the life of an obligate root parasite are as follows:

(i) The identification of a suitable host, thus coupling germination and seedling growth with the presence and direction of a potential host;

(ii) Gain of access to the host's nutrients and water supply; this process involves the production of a functional haustorium;

(iii)Completion of the life cycle on the host; this includes the establishment of parasitism and its maintenance until seeds are set.

The first two mechanisms are located in the parasite, while the third is located in the host. All the three different stages of the mechanism are expressed at different stages of the life cycle of the *Striga*. *Striga* and other root-parasitic plants have evolved highly efficient strategies to ensure successful reproduction. Key strategies include the dispersal of an enormous amount of tiny seeds of high longevity to establish an extremely persistent seed bank. These dust-like seeds are easily dispersed by wind, crop seeds, water and people (Nweze *et al.*, 2015). The seeds are triggered to germinate when there is a potential host, such as maize, close to them. When the seedlings germinate, they need to attach to host roots within 3-7 days, because the endosperm of *Striga* seeds can sustain growth/life only for the first 3-7 days (Berner *et al*., 1995). Within that time, *Striga* must successfully establish a parasitic relationship with the host plant or otherwise die.

The germination of *Striga* depends on the perception of germination stimulants released by host roots. In order to be responsive to germination stimulants, *Striga* seeds must go through a phase of moisture and high temperatures for 7–14 days, called 'conditioning'. If, during that time, no germination stimulant is perceived, *Striga* seeds fall into a secondary dormancy (Cardoso *et al*., 2011). Several germination stimulants have been isolated and include strigolactones, dihydrosorogoleone, sesquiterpene, kinetin,

coumarin, jasmonate, ethylene and fungal metabolites (Cardoso *et al*., 2011). Strigolactones are certainly the best studied and extremely potent inducers of *Striga* germination (Xie and Yoneyama, 2010). After germination of *Striga* seeds, the radical tip grows chemotropically towards potential host roots and on contact, *Striga* radicals stop growing, attach to host roots, form a haustorium and penetrate into the root cortex of potential hosts (Spallek *et al*., 2013). Haustorial development begins with the enlargement of cells in the protoderm or epidermis and underlying ground tissue and the initiation of haustorial hairs (Riopel and Baird, 1987). Haustoria may then form at the radicle or root apex and at lateral positions on the mature root of host plant upon induction by exogenous signals. Cells in the apex of the developing haustorium become specialized for penetration (Olonkwo and Nwoke, 1978), and growth through the host epidermis and cortex is rapid. Within 12 hours of attachment, reorganization of the *Striga* meristem is initiated. Essential for this step is the perception of haustoriainducing factors. Several naturally occurring haustoria-inducing factors have been isolated and their mode of action is best studied by following 2, 6-dimethoxy-pbenzoquinone (DMBQ) (Chang and Lynn, 1986).

In addition to chemical signals, a directional response of a physical touch of the growing radical to the host i.e. thigmotropic response is required for *Striga* to produce morphologically normal haustoria (Wolf and Timko, 1991). Within 24 hours after contact, rapid cell division of the radicale tip stops and a hypertrophic growth phase begins (Hood *et al*., 1998). Penetration of the host epidermis is mediated by the elongation of distal cells in the protoderm or epidermis and underlying ground tissue, followed by rounds of periclinal and anticlinal divisions of these cells, leading to growth into the cortex of host plants. When the host endodermis is reached, the most distal cells of the haustorium elongate and divide, thus forming a palisade arrangement

of cells. Break through the endodermis is often delayed, but once accomplished, vascular connections are established. In general, penetration is completed 48-72 hours after contact with a host root (Hood *et al*., 1998).

A detailed scanning electron microscopy study by Dorr (1997) showed that invading *Striga* cells perforate the host vascular system using a specialized structure, the osculum. Interestingly, no phloem-to-phloem connections have been observed between *Striga* and host plants. Once xylem-to-xylem connections are established, the cotyledons of *Striga* enlarge and break free from the seed coat within 24 hours (Hood *et al*., 1998). Haustorial maturation is completed when the host stele is penetrated, and vascular connections are established between the haustorium and the host (Saunders, 1933). The *Striga* seedling becomes largely autotrophic upon emergence from the soil but continues to procure water and nutrients from the host root system (Hood *et al*., 1998). After xylem-to-xylem connections have been established, the *Striga* plant grows upwards and adventitious roots are produced. These adventitious roots can form lateral (secondary) haustoria on the same or other host plants (Spallek *et al*., 2013).

Under natural conditions, host plants are usually parasitized by several *Striga* plants, and the parasites quickly become a metabolic sink for photo-assimilates and nutrients. Nitrogen levels are at least twice as high in *Striga* as in host plants (Agabawi and Younis, 1965). Depletion of nitrogen almost certainly affects host physiology and provokes lower host photosynthetic rates, which are frequently associated with *Striga* infections. Several photosynthetic parameters are reduced in host plants infected with *S. hermonthica*, including the electron transport rate through photosystem II and photochemical quenching (Rodenburg *et al*., 2008).

After emergence from the soil, *Striga* plants begin to photosynthesize. *Striga* leaves are characterized by a degenerated palisade cell layer and a relatively small number of chloroplasts per cell. Wickett *et al*. (2011) observed a relatively low expression of chlorophyll biosynthesis and photosynthesis-related genes. *Striga* obtains host photoassimilates through transpirational pull and this is due to the high transpiration rates observed in the plant and that further explains why high humidity is inhibitory to *Striga* growth. Indeed, *Striga* stomata show high conductance and respiration rates and little response to dark-induced closure (Press *et al*., 1987). Relative to the host plant, *Striga* has a disadvantageous leaf surface ratio and might compensate for this with higher stomatal conductance (Press *et al*., 1987). Surprisingly, when water depletion was investigated under controlled experimental conditions of *Striga*-infected maize plants, no significant increase in water use was observed until the very late stage of infection (63 days post-infection) (Taylor and Seel, 1998; (Nweze *et al*., 2015).). However, during the final stages of infection, maize plants used nearly 50% more water than control plants (Spallek *et al*., 2013).

2.2.3.3 Control of *Striga*

Striga is a root parasitic plant and 35 species exist globally (Berner *et al*., 1995). Eighty percent of the species can be found in Africa but not all of them affect crop production. United States of America and Australia are among the developed countries also affected by this parasitic weed, but in these countries methods to combat *Striga* have been developed which include chemical inputs that are too expensive for the African farmers. *Striga* causes severe yield losses, sometimes the farmers lose 100% of their harvest when forced to abandon highly infested fields (Berner *et al*., 1995). Therefore, it has a major economic impact for smallholder farmers, as it decreases the income significantly. The weed also lowers the food supply for many households as it causes

major damages on the staple food and affects families whose food consumption is dependent on the harvest, i.e. subsistence farmers. Also, as infested areas and levels of *Striga* are expected to increase in the future, due to continuous monoculture of cereals in combination with low organic and mineral fertilizer rates (Teka, 2014). Especially in the non-fertile semi-arid region of Africa, controlling *Striga* has therefore become a huge task considering the seed production rate and the fact that the seed remains viable in the soil for up to 20 years (Ikie *et al*., 2006). This can lead to a rapid build-up of the seed bank in the soil, once fields have been contaminated (Van Mourik *et al*., 2008). Several methods to combat *Striga* exist today and this includes the use of resistant maize, intercropping with legumes, fallow, suicidal germination, pesticides (De Groote *et al*., 2007; Atera *et al*., 2011). However, adoption of these methods is often slow; one reason for this is that farmers doubt them (Khan *et al.,* 2009) and, returns of the new methods in terms of higher yield do not appear immediately but the cost do (Khan *et al.,* 2008*)*. Control of *Striga* has proved difficult using cultural practices or herbicides because *Striga* produces many seeds which can remain viable in the soil for so many years (Parker and Riches, 1993). Earlier report by Heller and Wegmann (2000) has demonstrated that for the completion of each of the critical stages of the life cycle of *Striga*, enzymes play a major role. Therefore, maize varieties with the genes controlling the expression of parasitic weed germination and development would be very important in controlling *Striga* infestation. Thus, a practical and sustainable way to control *Striga* is to use resistant and or tolerant varieties. *Striga* resistance is the ability of the host root to stimulate *Striga* germination but at the same time prevent attachment of the seedlings to its roots or to kill the seedlings when attached (Sibhatu, 2016). On the other hand, *Striga* tolerance is characterized by lower *Striga* damage to a variety as a result of its ability to withstand the effects of the parasites that are already attached to the host (Badu-Apraku *et al.,* 2008). It has been generally accepted that *Striga* control is more

likely to be achieved by combining a range of individual component technologies into a program of integrated *Striga* control to provide more flexible and sustainable control over a wide range of biophysical and socio-economic environments (Dashiell *et al*., 2000).

2.2.4 Influence of drought on maize production

With global climate change and uncertainties in precipitation patterns, food security may become more serious than in the past (FAO, 2008), yet few economically-viable approaches exist to support crop production under drought (Li *et al*., 2000). Cereal grains are the most important source of calories for the majority of human population with maize and wheat alone contributing to more than 50% of global cereal production of about 713 million tons of grain production (Daryanto *et al.*, 2016). Although in the arid and semi-arid areas of Africa, lack of water and soil degradation and loss are usually cited among the major causes of low productivity in maize production (Nin Pratt *et al.*, 2011). However, Rockstrom *et al*. (2007) noted that there is sufficient water for growing crops, even in dry regions, thus, crop yields are not affected by nonavailability of water per se but by long dry seasons, strong weather variability and unpredictable rains during critical crop growth stages which makes it harder to control and use water resources.

Drought refers to circumstances when natural or managed water systems do not provide enough water to meet established human and environmental uses because of natural shortfalls in precipitation or stream flow (Robert *et. al*., 2000). Drought is a worldwide problem and dangerous for arable crop growth and subsequently for food security (Jaleel *et al.*, 2009). During the past ten years, three out of every four global drought events occurred in Africa (AATF, 2010). Drought has become a widespread

phenomenon across large areas of sub-Saharan Africa in particular and Africa as a whole.

2.2.5 Interaction of low soil nitrogen and *Striga*

The increasing incidence of *Striga* has been attributed to poor soil fertility, moisture stress, intensification of land use through continuous cultivation and an expansion of cereal production (Parker, 2008). About 10-100% loss in maize grain yield has been attributed to *Striga* parasitism (Lagoke *et al.,* 1996). Years of farming without adequate use of fertilizer has resulted in the depletion of vital soil nutrients required to support plant growth in SSA (Sanchez, 2010). While current evaluations of yield loss as an effect of low-N are not available, low-N is still the most important limitation to maize production (Abe *et al*., 2013).

Cechin and Press (1993), indicated that nitrogen affects *Striga* germination and attachment to the host root system and therefore the partitioning of photosynthates. The consequences of low-N on *Striga* parasitism in maize has had conflicting results over the past years. Kim and Adetimirin (1997) and Kim *et al.* (1997) reported that adequate N application reduced *Striga* infestations. In contrast, Smaling *et al.* (1991) and Kamara *et al.* (2007) reported that availability of adequate N had no effect on *Striga* infestation.

2.3 Breeding for stress tolerant maize in Africa

Africa's population is increasing rapidly, but agricultural production can barely keep up. Options for increasing crop areas are limited, and the purchasing power of most of its population is low. Therefore, yield increases are essential to ensure food security. Yield increases are expected from two types of technologies: new varieties and better soil fertility management. There is little doubt that maize seed technical change has occurred in SSA. African smallholders have readily used well-adapted, improved maize

in a number of locations and time periods, as documented historically by maize researchers and social scientists (Byerlee and Eicher, 1997). There is no doubt that as the land frontier diminishes in many parts of the continent, sustainable development in societies that remain primarily agrarian will require productivity gains rather than area expansion. As the effect of climate change advances and maize production continues to expand into marginal production areas, the effects of drought, *Striga* and low N stress will remain major challenges in places where most farmers have limited capacity to invest into inputs (Cairns *et al*., 2013). Investment in maize research is required to produce a new generation of improved varieties that are drought tolerant, pest resistant, and nutrient efficient in Africa. The adoption of stress tolerant maize could generate US$362 to $590 million within the maize production and consumption sector which can seriously reduce poverty by 5% within SSA (Kostandini *et al*., 2013).

In modern breeding programs, varieties are often developed by crossing parental genotypes possessing the most desired traits (e.g., yield, early flowering, vigor, plant architecture), and selecting offspring under optimal growth conditions. Genotypes selected for high performance in high-input conditions often do not maintain those same high yields under low-input conditions partly due to lack of natural genetic variation of traits advantageous in stressful environment (Murphy *et al*., 2005). Grain yield under stress and optimal growing conditions are controlled by different physiological mechanisms (Blum, 1997; Ceccarelli, 1996; Badu-Apraku and Fakorede, 2017). Therefore, to get the highest expression of genetic variation for relevant traits that could be exploited in stress tolerance breeding programs, genotype evaluations should be conducted in an environment best suited to the specific agricultural ecosystems (Bänziger *et al.*, 2000), which will allow for maximum production in that setting (Fess *et al*., 2011).

2.3.1 Genetic variability for nitrogen use efficiency in maize

Nitrogen use efficiency (NUE) is defined as grain yield *per* unit of nitrogen (N) supplied and expressed as the product of N uptake efficiency (NUpE) and N utilization efficiency (NUtE) indexes (Almeida *et al*., 2018). The goal for NUE improvement is to increase yield potential without additional N input, reduce N input without affecting yield significantly and increase low-N tolerance with very low-N input (Mi *et al*., 2012). Generally, N uptake and N utilization are the most important components of NUE. According to Bertin and Gallais (2000) and Presterl *et al*. (2002), the N uptake efficiency contributes more to NUE variation under low and high N availability, while N utilization efficiency contributes more under low N condition. From a physiological perspective, NUE is also influenced by the N dynamics within the plant. Coque and Gallais (2007) observed that after silking, N is accumulated within the grain by postsilking N uptake and N remobilization from the stover (Gallais and Coque, 2005). Additionally, under high N condition, the variation in NUE is mainly due to post-silking N uptake, whereas under low N condition, N remobilization also contributes to NUE variation (Gallais and Coque, 2005). There is wide variation within maize germplasm in terms of nitrogen nutrition particularly for low-N tolerance and NUE (Bänziger and Lafitte, 1997). Genotypes with a short anthesis-silking interval and prolific genotypes seem to have the ability to remobilize N from the stover to the grain efficiently, particularly in the early stage of embryo development, avoiding embryo or ear abortion (Gallais and Coque, 2005). Leaf area duration appears to be an important factor for post-silking N-uptake and thus grain filling and is favourable for NUE whatever the N input (Gallais and Coque, 2005). Maize genotypes with high stay green abilities have greater tolerance to post-silking environmental stresses (Tollenaar *et al*., 1994), which include reduction in N uptake and prolonged leaf longevity (Hay and Porter, 2006)

which sustain photosynthetic activity at a time of decline but high crop N demand (Kosgey *et al*., 2010). These attributes make stay green characteristic an important component of genetic variation in NUE in maize (Bänziger *et al*., 2000). The presence of genetic variation in NUE implies that NUE could be assessed and improved genetically through selection (Mi *et al.*, 2012), making it possible to breed new cultivars possessing better adaptation to nitrogen deficient environments than what exist now.

Studies on genetic variatbility for NUE should explore two key areas: firstly, it has to assess the existence of genetic variation for NUE for a given nitrogen level; Secondly it has to also determine the existence of Genotype x Nitrogen (G xN) interactions for well-fertilized and nitrogen deficient environments. Genetic variation for NUE is expressed differently at low and high N-input. Thus, genes for adaptation to N stress can only be observed under sufficiently low-N input (Bänziger et al., 2000, Adu *et al*., 2018). Studies by Bänziger and Lafitte (1997) and Presterl *et al*. (2002) have demonstrated that the maximum genetic advance at low N-input is better achieved when selection is done in low-N environments (Gallais and Coque, 2005). In low-N environments, genetic variance is usually reduced. Studies by Bertin and Gallais (2000) under both low and high N inputs showed a reduction in genetic variance in NUE under low-N input. The authors also observed a high association between grain yield and kernel number across varying nitrogen levels and a complete lack of G x N interaction for plant traits at silking. These results indicated that grain yield is mainly influenced by kernel numbers which is determined by nitrogen use.

Under sufficiently contrasted N environments, correlation between high and low N inputs tends to decrease as nitrogen stress increases (Gallais and Coque, 2005). Which is associated with yield reduction at low N-input. Bänziger *et al*. (1997) found lower

genetic correlation of 0.38 between grain yields under low and high nitrogen conditions, due to a yield reduction of 54% under low-N conditions. Presterl *et al*. (2003) also reported relatively high yield reduction at low N conditions, with a lower genetic correlation at higher N-stress. The presence of genotype by nitrogen interaction depends on the kind of germplasm under consideration, In the Presterl *et al*. (2003) studies, inbreds developed from landraces had high genetic variability. Lafitte *et al*. (1997) evaluated the grain yield, N uptake, and N partitioning patterns of 171 landraces under adequate and limited levels of soil N, a principal component analysis of key traits related to N uptake and allocation patterns grouped the 171 landraces into six different clusters. The performance of the different clusters across the different N levels indicated specific adaptation to either high or low N environments in which total N accumulation, N partitioned to the grain, and grain N concentration varied independently. On the contrary, Gardner *et al*., (1990) found no G x N interaction among hybrids derived from elite materials. The absence of G x N interaction among the hybrids in the studies of Gardner *et al*., (1990) was attributed to lost of specific genes for adaptation to low N conditions through genetic drift resulting from selection in only favourable conditions for over 5 decades of selection (Gallias and coque, 2005). In the Lafitte *et al*. (1997) experiments, average grain yield of 26 improved cultivars was 56% higher than the grain yield of 38 landraces under both high and low N environments. However, the landraces had greater grain N concentrations at both N levels, thus, the authors concluded that landraces can contribute useful traits for stable production in N-limited environments but selection should not be based solely on grain yield (Lafitte *et al*.,

1997).

2.3.2 Use of secondary traits and selection index in stress tolerant maize breeding

The indirect selection of genotypes in optimal environments for performance in other contrasting environments is usually complicated by the presence of genotype × environment interaction (GEI), Genotype × environment interaction due to the relative differences in the response of genotypes to different environments reduces the correlation between phenotypic and genotypic values (Comstock and Moll 1963) under stress environments. In maize, the relative effect of GEI on a genotype vary from one trait to the other with pronounce effects on polygenic traits such as grain yield. Most research outputs by CIMMYT have showed that variety selection based on grain yield alone under drought and low-N environments are usually inefficient because heritability of grain yield under stressed environments is low (Edmeades *et al.*, 1997). Under such conditions, the use of secondary traits have improved selection effeiency in maize (Edmeades *et al*., 1998). According to Edmeades *et al.* (1998) an ideal secondary trait should be: Genetically associated with grain yield under stress; highly heritable; genetically variable; cheap and fast to measure; stable within the measurement period, not associated with a yield penalty under unstressed conditions, observed at or before flowering, so that undesirable parents are not crossed and a reliable estimator of yield potential before final harvest (Bänziger *et al.*, 2000).

Index Selection is a method of artificial selection in which several desirable traits are selected simultaneously (Villanuev and Kennedy, 1993). Wricke and Weber (1986) and Van Vleck (1993) present insightful review on the the theory and application of selection indices. Multiple-trait selection index allows breeders to consider the mutual effects of several traits on yield at the same time, rather than the independent effects of the individual traits involved (Adu *et al.*, 2016). Traditionally, a selection index based on increased grain yield, reduced barrenness, reduced anthesis-silking interval (ASI)),

delayed leaf senescence, good plant and ear aspects is used to select for high yielding genotypes with tolerance to low-N and drought (Bänziger *et al*., 1999; Menkir and Akintunde, 2001; Badu-Apraku *et al*., 2011a). For *Striga* resistance improvement programs, a selection index which combines increased grain yield measured under *Striga*-infested and *Striga*-free environments, reduced *Striga* damage, reduced number of emerged *Striga* plants, good ear aspect and increased number of ears per plant (EPP) is used (MIP, 1996; Menkir and Kling 2007; Badu-Apraku and Fakorede, 2017).

The use of these selection indices has been very successful in the past (Monneveux *et al*. 2006, Badu-Apraku and Fakorede, 2017). However, recent studies involving the same selection indices have reported inconsistent results. For instance, contrary to reports by Menkir and Akintunde (2001) and Badu-Apraku *et al.* (2004b; 2011a), results of Badu-Apraku *et al.* (2012) indicated that leaf death is not a reliable trait for selecting genotypes that are drought tolerant, and EPP and ASI are also unreliable characters for identifying low-N tolerant genotypes. The authors identified plant height, days to silking, and days to anthesis, which are not included in the low-N selection index as reliable for selecting early maturing inbred lines under low-N conditions. Reports by Badu-Apraku *et al. (*2005, 2006, 2007) and Badu-Apraku and Fakorede (2017) indicated that number of emerged *Striga* plants which has strong association with grain yield in late and intermediate maturity groups of maize varieties (Gethi and Smith, 2004; Menkir and Kling, 2007, Yallou *et al*., 2009; Badu-Apraku and Fakorede, 2017), has a weak phenotypic and genotypic correlations with grain yield in early group. Badu-Apraku *et al*. (2012a) found that after four cycles of S_1 family selection in an extra-early maturing population under *Striga* infestation, yield was not correlated with other traits at C_0 but was significantly correlated with EPP, *Striga* damage, and the number of emerged *Striga* plants in advanced cycles (Badu-Apraku and Fakorede,

2017).

A review of these contradictory results showed a trend dependent on the type of germplasm under selection, the kind of trait and the level of improvement already achieved in the desired germplasm. Since there is the possibility for every set of breeding lines to have unique trait associations, validation of long established secondary traits and assessment of the possible use of other traits in the selection of high yield and stress tolerant genotypes is relevant in breeding programs (Bolanos and Edmeades, 1996; Monneveux *et al.*, 2008).

2.3.3 Genotype by environment interaction and stability analysis

One of the main challenges in statistical genetics is to find superior genotypes over a wide range of agro-ecological conditions and also over a number of years (Rodrigues, 2018). Genotype by environment interaction is defined by the change of the genetic ranking of genotypes with the environment; thus, a genotype that is superior in nonstressed environments may yield poorly under stressed-environments. In maize breeding, the search for genotypes with high grain yield adapted to varied environments is one of the most important objectives for breeders. This is because GEI complicates selection of genotypes with wide adaptability and also reduces genetic gains and adversely affects cultivar recommendations (Souza *et al*., 2009). The GEI can be expressed either as crossovers, when two different genotypes change in rank order of performance when evaluated in different environments, or as inconsistent responses of some genotypes across environments without changes in rank order (Rodrigues, 2018). The study and understanding of these interactions are a major challenge, particularly when the aim is to improve polygenic traits such as grain yield across environmental gradients (Annicchiarico, 2009; Crossa, 1990; van Eeuwijk *et al*., 2016).

A wide range of statistical methods have been developed to explore multi-location/year trials data to provide better understand of GEI. This is to help breeders to make predictions for different environments/locations and years (Malosetti *et al.,* 2010; Kang and Gauch, 1996). In multi-environment yield trials, the classic model for analysing the total yield variation contained in GEI observations is the analysis of variance (Fisher, 1918). The within-environment residual mean square measures the error in estimating the genotype means due to differences in environmental factors from one plot to another (Tiwari, 2017). After removing the replicate effect when combining the data, the GE observations are partitioned into two sources: (a) additive main effect for genotypes and environments and (b) non-additive effects due to GEI. A major limitation of the combined analysis of variance (ANOVA) of multi-environment trials is that it does not explore any underlying structure within the observed non additivity (GEI), also, ANOVA does not determine the pattern of response of genotypes and environments. Therefore, without further analyses, the valuable information contained in GEI degrees of freedom is virtually wasted. Usually, combined ANOVA is routinely used as the first step to identify the existence of GEI from replicated multi-environment trials. Once a significant GEI variance is obtained other methods for measuring the stability of genotypes are used to identify the stable genotype (s). The several methods available for exploration and analysis of GEI can be classified into four main groups as the analysis of components of variance, stability analysis, multivariate methods and qualitative methods (Vishakha 2017).

Stability analysis methods determine the stability of genotypes based on the GEI available. The more frequently used of the stability analysis methods are the Francis and Kannenberg‟s coefficient of variability (Francis, 1977), Lin and Binns cultivar performance measure (Lin and Binns, 1988), Shukla's stability variance parameter

(Shukla, 1972), Finlay and Wilkinson's joint regression analysis (Finlay and Wilkinson, 1963) and Wricke's Eco valence (Wricke, 1962; 1964). Multivariate analysis methods elucidate the internal structure of mult-environment trials data from which hypotheses can be generated and later tested by other statistical methods (Gauch, 1982a & b). Multivariate analysis is appropriate for analyzing two-way matrices of genotypes (G) and environments (E). The response of any genotype in E environments may be conceived as a pattern in E-dimensional space, with the coordinate of an individual axis being the yield or other metric of the genotype in one environment.

Principal component analysis (PCA) is the most frequently used multivariate method (Crossa, 1990; Purchase, 1997). Additive main effects and multiplicative interaction (AMMI) is also commonly used, AMMI integrates the analysis of variance and principal components analysis into a unified approach (Gauch, 1988). The AMMI Stability Value (ASV) by Purchase (1997) and the GGE biplot analysis (Genotype + Genotype by Environment) by Yan *et al*. (2000) are also used by researchers. The multivariate methods allow graphical representation in their outputs. All these methods have their advantages and limitations, as stated earlier the combined ANOVA have a merely additive model, it identifies GEI as a source but does not analyse it; PCA analysis is a multiplicative model and hence contains no sources for additive genotype or environment main effects; and linear regression (LR) analysis is able to effectively analyse interaction terms only where the pattern fits a specific regression model. The consequence of fitting inappropriate statistical models to yield trial data is that the interaction may be declared insignificant, although a more appropriate analysis would find agronomically important and statistically significant patterns in the interaction.

Since ANOVA, PCA, and LR are sub-cases of the more complete AMMI model, AMMI offers a more appropriate first statistical analysis of yield trials that may have a GEI.

Since 2004, the use of graphical techniques such as biplots (Gabriel, 1971), GGE biplots, PCA and AMMI models have increased sharply in number. Yan *et al*. (2007) compared GGE Biplot and AMMI analyses and concluded that both GGE Biplot and AMMI analyses combined rather than separated G and GxE in mega-environment analysis and genotype evaluation. However, the GGE Biplot was superior to the AMMI graph in mega-environment analysis and genotype evaluation, because it explained G + GxE more effectively and had the inner-product property of the biplot. Furthermore, the discriminating power x representativeness view of the GGE Biplot was effective in evaluating test environments, which was not possible with AMMI analysis. Gauch *et al.* (2008) reviewed AMMI and GGE analyses, they concluded that the AMMI megaenvironment graph incorporated more of the genotype main effect and captured more of the GEI than did the GGE Biplot graph, and thereby displayed the "whichwon-where" pattern more accurately for complex datasets. The authors also repoeted that when the GEI is captured well by one principal component, the AMMI graph of genotype nominal yields described winning genotypes and adaptive responses more simply and clearly than the GGE Biplot. Thus, for genotype evaluation within a single mega-environment, a simple scatterplot of mean and stability was more straightforward than the mean x stability view of a GGE Biplot. Choukan (2010) evaluated METs data of 14 maize inbred lines based on AMMI and GGE biplot analysis. He reported that AMMI was effective alternative method for assessing the suitable genotype, while GGE biplot was effective tool for the mega-environment analysis (which-won-where pattern), genotype evaluation (mean performance and stability and environment evaluation (to discriminate among genotypes in targeted environment). on the contrary, Miranda *et al* 2009 found that both AMMI and GGE biplots are adequate to explain the GEIs in nine popcorn cultivars sown on four different dates in the 1998-1999 and 1999-

2000 seasons.

2.4 Use of molecular markers in genetic diversity studies of maize

Plant breeders often require detailed information on the level and pattern of genetic diversity in breeding materials and the relationship among them to make informed decisions on the breeding processes. Several researchers have highlighted the importance and the need for accurate assessment of genetic diversity in a cultivar development program (Hallauer and Miranda, 1988; Barrett *et al.,* 1998; Thompson *et al.,* 1998; Mohammadi *et al*., 2003; Reif *et al*., 2003; Flint-Garcia *et al*., 2009). Genetic diversity assessment is useful as it allows the assignment of inbred lines to heterotic groups and the analysis of genetic variability in breeding materials. It is possible to decide on the introgression of desirable genes from diverse germplasm into available genetic base (Badu-Apraku and Fakorede, 2017); the identification of diverse parental combinations to create segregating progenies with maximum genetic variability for further selection and the estimation of genetic diversity loss during conservation or selection programs (Xia *et al.,* 2004; Semagn *et al*., 2012; Badu-Apraku and Fakorede, 2017).

The assessment of genetic diversity within and between plant populations is routinely performed via different marker techniques such as morphological, biochemical and deoxyribonucleic acid (DNA) markers (Govindaraj *et al*., 2014). DNA based markers are preferred over morphological and biochemical markers because these markers are not affected by environment factors or the developmental stage of the plant (Govindaraj *et al.,* 2014). DNA markers have been an indispensable tool for characterizing genetic resources and providing breeders with more detailed information to assist in selecting diverse parents (Collard and Mackill, 2008). In maize, various molecular markers have been extensively used for genetic diversity analysis in order to study the correlation

between genetic distance and hybrid performance (Badu-Apraku and Fakorede, 2017), heterosis, and combining abilities (Betran *et al.*, 2003a; Liu *et al*., 2003).

Available DNA markers include Restriction Fragment Length Polymorphisms (RFLPs), Random Amplified Polymorphic DNA (RAPD), Simple Sequence Repeats (SSRs), and Single Nucleotide Polymorphisms (SNPs) (Warburton *et al,* 2008, 2010; Xu *et al*., 2009; Shiferaw *et al*., 2011; Menkir *et al.,* 2010; Semagn *et al*., 2012). An ideal marker system should be highly polymorphic, codominant, accurate, reproducible, high-throughput and low cost, both in terms of capital investment and cost per assay (Jones *et al.,* 2007). it should also be reproducible along laboratories (Weising *et al*., 1998). Among the DNA markers, SSRs have been widely used in plant genetics and breeding, because they are co-dominant, easy to score, and highly abundant (Xu *et al*., 2013). This marker type offers several advantages over other markers including higher level of reliability, reproducibility, discrimination, standardization and cost effectiveness (Xia *et al*., 2004; Jones *et al.,* 2007). Menkir *et al.* (2005) studied the genetic diversity of maize inbred lines with different reactions to *Striga hermonthica* using AFLP and SSRs and found that the inbred lines were separated into groups based on the source population from which they were derived. Akaogu *et al*., (2012) examined the effects of genetic diversity of extra-early inbred lines on hybrid performance based on SSRs, and reported that correlations between the SSR-based GD estimates of parental lines and the means observed in F_1 hybrid under *Striga* infestation and optimal growing conditions were not significant for grain yield and other traits except for anthesis-silking interval under optimal conditions. More recently, SNPs have become the most used marker type (Raza *et al.,* 2016). These markers have the following properties that makes them desirable: (1) low-cost per data point; (2) high genomic abundance; (3) locus-specificity; (4) co-dominance; (5)

potential for high throughput analysis, and (6) lower genotyping error rates (Jones *et al.,* 2007; Yan *et al.,* 2010; Semagn *et al.,* 2012). Single-nucleotide polymorphism markers have been used in a number of applications including genetic diversity analysis, QTL mapping, linkage disequilibrium analysis, genomic-wide association studies, genomic selection/prediction and marker assisted selection (Collard and Mackill, 2008). Using SNP markers, Mengesha *et al*. (2017) characterized 128 drought tolerant and *Striga* resistant maize inbred lines under drought and *Striga*-infested environments and identified four distinct groups. Wen *et al.,* (2011) classified 359 advanced drought, low-N, soil acidity, and pest and disease resistant maize inbred lines from IITA and International Maize and Wheat Improvement Center (CIMMYT) into nine subgroups using 1260 SNP markers. The authors detected that the nine main subgroups were influenced by pedigree information, environmental adaptation, and breeding scheme. Wu *et al*., (2016) studied the genetic diversity and population structure of 538 CIMMYT inbred lines and six temperate inbred lines using genotyping-by-sequencing SNPs. Their results indicated wider genetic distance and low kinship coefficients among the CIMMYT lines. The authors identified clear population structure and genetic divergence between the temperate subgroup and tropical subgroups, including major environmental adaptation groups (Lowland Tropical, Subtropical/Mid-altitude and Highland Tropical subgroups) among the CIMMYT lines, with greater genetic diversity among the tropical subgroups than that of the temperate subgroup.

2.5 Combining ability studies and heterotic groupings of maize germplasm

Combining ability estimates are important genetic attributes in classifying inbred lines; defining heterotic groups and assessing the performance of inbred lines in hybrid combinations (Kauffman *et al.,* 1982; Menkir *et al.,* 2004; Melani and Carena, 2005;

Fan *et al.,* 2006). In grouping inbred lines into heterotic groups the following methods are usually used: Specific combining ability (SCA) effect of grain yield per se, heterotic group's SCA and general combining ability (GCA) (HSGCA), GCA of multiple traits (HGCAMT) and genetic distances (GD) estimated by molecular markers (Fan *et al.* 2008, 2009; Badu-Apraku *et al.,* 2013). Combining ability is an estimation of the value of genotypes based on their offspring performance in some definite mating design (Allard, 1960). It allows the partitioning of the genetic influence of a genotype into additive and non-additive components.

General combining ability is the average performance of a line in a series of hybrid combinations and SCA is the deviation of crosses on the basis of average performance of the inbred lines involved (Sprague and Tatum, 1942; Fasahat *et al.,* 2016). General combining ability (GCA) is largely additive in its effects (Griffing, 1956), while SCA is due to dominance and epistasis, and other non-additive effects (Falconer and Mackay, 1996). Both GCA and SCA interacts significantly with the environments in which the genotypes are tested, SCA is the most influenced by environmental changes (Anderson, 1960; Pacheco *et al*., 1999; Plaisted *et. al*, 1962; Kalsy *et al*, 1970). For this reason, Rojas and Sprague (1952) suggested the inclusion of Genotype x Environment interactions (GEI) in the estimation of SCA effects for more stable and reliable estimates. Numerous genetic studies in crops have been conducted using SCA effects of grain yield per se and HSGCA. Some authors have indicated the difficulty in classifying tropical inbred lines into distinct groups based only on the results of combining ability studies (Badu-Apraku *et al.,* 2016). A major drawback of heterotic grouping, whether by SCA or HSGCA, is that it is usually based on one trait, primarily grain yield. However, grain yield is a polygenic trait highly influenced by environment and has low heritability especially under stressful environments. Therefore, heterotic grouping based on grain yield alone is usually not effective (Fan *et al.,* 2009; Akinwale

et al., 2014). To overcome this, Badu-Apraku *et al.,* (2013b) proposed the high GCA effect of multiple traits (HGCAMT) to accommodate the effects of grain yield along with its relevant component traits for a more effective and reliable groupings. Since this approach measures multiple traits of test inbred lines with significant GCA effects across environments where they are tested, a more precise classification of the inbred lines into heterotic groups could be achieved, particularly in a situation where inbred lines and hybrids are being developed for resistance or tolerance to multiple stresses (Badu-Apraku *et al.,* 2013b).

Molecular markers have been found to be a powerful tool for defining heterotic groups and determine the genetic diversity between parental lines at the DNA level. Molecular markers are also used in marker assisted-selection programs to complement existing conventional breeding approaches to increase the precision and fast track the selection of target genotypes, resulting in quicker line/variety development and variety releases (Ribaut and Hoisington, 1998). Although, present reports indicate that it is not yet possible to predict the exact level of heterosis expected for a given cross based on genetic distance estimates (Lee *et al*., 1989; Benchimol *et al.,* 2000; Shieh and Thseng, 2002; Menkir *et al.,* 2010), successes have been reported for assigning parental lines to proper heterotic groups (Lanza *et al.,* 1997 and Balestre *et al.,* 2008). To improve the effectiveness of molecular markers for classifying lines into distinct heterotic groups, Jordan *et al.* (2003) proposed the potential use of a combination of smaller subsets of DNA marker data and phenotypic data to select heterotic hybrids. Work done so far involving the use of phenotypic and molecular data showed that the use of HSGCA is more effective than the use of SCA effects of grain yield alone or molecular markers for classifying inbred lines into distinct groups (Fan *et al.,* 2004; Badu-Apraku *et al.,*

2013b, 2013c). Similarly, Akinwale *et al*. (2014) in their report on the effectiveness of SCA effect of grain yield, HSGCA, and microsatellite markers for assigning inbred lines into heterotic groupings, ranked the HSGCA method as the best, followed by the molecular marker method. Reports by Badu-Apraku *et al*. (2013b) indicated that heterotic groupings based on the HGCAMT method was comparable to the groupings based on SSR markers but superior to the groupings based on SCA effects of grain yield. Badu-Apraku *et al*. (2016) examined the combining ability of 17 early-maturing yellow maize inbred lines from IITA and CIMMYT under drought, low-N and optimal conditions. The 17 inbreds were classified into four heterotic groups across each environment by HSGCA and SNP-GD while HGCAMT method placed them into three groups. The authors concluded that HGCAMT was the most efficient heterotic grouping method followed by HSGCA and then SNP-GD method, and recommended the HGCAMT for grouping the numerous IITA inbreds that are yet to be field tested.

C

HAPTER THREE

3.0 Genetic diversity in early maturing maize inbred lines using simple sequence repeats (SSRs) and single nucleotide polymorphism (SNPs) markers

3.1 Introduction

Molecular markers allow precise and rapid assessment of genetic diversity of crop varieties. Simple sequence repeats and SNPs are both popularly used in recent crop genetic studies. Individual SNP markers, being bi-allelic, have lower information content than SSRs which is multi-allelic. However, SNP markers are increasing becoming popular particularly because they occur at much higher density in the genome, are amenable to high-throughput methods such as genotyping arrays, and have lower genotyping error rates (Kennedy *et al.*, 2003 and Schlotterer C, 2004). The major differences between SSRs and SNPs are associated with their mutational models and neutrality processes (Vignal *et al*., 2002). The polymorphisms of SSR are caused by replication slippage, while polymorphism of SNP are generated by point mutation (Singh *et al.*, 2013). Therefore, the two marker types can provide different views of the structure of a given population. However, the choice of either one or the other marker type, and the number of loci needed has been a big debate, as cost plays a major role as well as the purpose of study and the evolutionary history of the populations under investigation (Varshney *et al*., 2009).

Studies on the comparative utilization of either SSR or SNP markers reveals that SSR markers with moderate density is more effective for diversity and population structure analyses in maize but as the number of SNP markers increases the results obtained are

comparable (Hamblin *et al.*, 2007; Jones *et al.*, 2007). However, very limited research has been conducted into the effectiveness of both SSR and SNP markers (Badu-Apraku and Fakorede, 2017) in characterizing maize inbred lines of the early and extra-early maturing groups of IITA. For example, Elohor (2013) examined the level of genetic variability among 87 IITA and nine CIMMYT early-maturing inbred lines. The author reported that the SNP markers were more effective in population structure analysis, whereas the SSR markers were more efficient for genetic diversity studies. Encouraged by this result, there is the urgent need to utilize both SSR and SNP markers to assess the genetic differences and relationships among the new extra-early and early maturing white and yellow maize inbred lines that have been recently developed by IITA for their effective classification into heterotic groups and also to serve as a guide to parent selection for further hybrid development. The present study was conducted to determine the genetic diversity and population structure of white and yellow maize inbred lines derived from different source populations selected from a panel of inbred lines of the IITA Maize Improvement Program using SSR and SNP markers.

3.2 Materials and methods

3.2.1 Germplasm

The 100 inbred lines used in this study were bred by the West and Central Africa Collaborative Maize Research Network/International Institute of Tropical Agriculture (WECAMAN/IITA) (Tables 3.1). They are resistant/tolerant to *Striga* and maize streak virus (MSV), and/or tolerant to drought. The inbred lines were extracted from twelve broad-based and two narrow-based source populations developed from both local and exotic germplasm identified based on several years of extensive testing for adaptation to the Guinea and Sudan savanna agro-ecologies of West and Central Africa. The first generation of inbred lines were obtained following six generations of self-pollination

in four early (TZE-W Pop DT STR C0, TZE-Y Pop DT STR C0, TZE Comp5-Y C6 and WEC STR) and two extra-early (TZEE-W Pop DT STR C0 and TZEE-Y Pop DT STR C0) broad-based populations with varied levels of drought tolerance and *Striga* resistance. A few inbred lines extracted from the two extra-early source populations, were categorized as early maturing because the flowering dates were typical of lines of the early maturing group. A second generation of inbred lines were developed from two F_2 populations derived from the bi-parental crosses, TZEI 1 x TZEI 2 and TZEI 11 x TZEI 8 which involved elite parental inbred lines from two of the four broad-based early maturing populations. Another set of inbred lines were extracted from two other bi-parental crosses, TZE-W Pop x 1368 STR and TZE-W Pop x LD. The second generation of inbred lines were in all cases obtained following 6-7 cycles of selfpollination and selection for drought tolerance and/or resistance to *Striga*.

Table 3. 1 List of inbred lines used in the study and their respective endosperm colour and pedigree information

Name	Endosperm Colour	Pedigree and selection history	Name	Endosperm colour	Pedigree and selection history
TZEI 344	White	(TZEI 1 x TZEI 2) S6 inb 109-4/10-1/2-1/1	TZdEI 139	White	TZE-W POP STR 104 S5 17/160-1/1
TZEI 295	White	(TZEI 1 x TZEI 2) S6 inb 13-1/2-2/3-1/1	TZdEI 100	White	TZE-W POP STR 104 S5 20/208-1/2-1/3-1/2-4/4
TZEI 298	White	(TZEI 1 x TZEI 2) S6 inb 13-2/2-3/3-1/1	TZdEI 157	White	TZE-W POP STR 104 S5 22/160-1/3
TZEI 365	White	(TZEI 1 x TZEI 2) S6 inb 136-2/5-1/4-1/1	TZdEI 69	White	TZE-W POP STR 104 S5 45/208-1/2-1/1-4/7-4/9
TZEI 376	White	(TZEI 1 x TZEI 2) S6 inb 189-3/4-1/3-1/1	TZdEI 92	White	TZE-W POP STR 104 S5 6/208-1/2-1/2-1/1-3/4
TZEI 378	White	(TZEI 1 x TZEI 2) S6 inb 190-1/9-1/3-1/1	TZdEI 131	White	TZE-W POP STR 104 S5 83/208-1/1-2/2-3/4-3/4
TZEI 379	White	(TZEI 1 x TZEI 2) S6 inb 190-1/9-2/3-1/1	TZdEI 82	White	TZE-W POP STR 104 S5 98/208-2/2-2/2-1/2-2/3
TZEI 402	White	(TZEI 1 x TZEI 2) S6 inb 239-1/3-2/2-1/1	TZdEI 222	White	TZE-W POP STR 108 S5 183/198-1/1-3/3-1/1-6/9
TZEI 413	White	(TZEI 1 x TZEI 2) S6 inb 274-3/3-1/3-1/1	TZdEI 215	White	TZE-W POP STR 108 S5 195/198-1/2-2/2-1/2-10/10
TZEI 323	White	(TZEI 1 x TZEI 2) S6 inb 45-1/3-1/4-1/1	TZdEI 221	White	TZE-W POP STR 108 S5 195/198-1/2-2/2-2/2-1/6
TZEI 448	Yellow	(TZEI 11 x TZEI 8) S6 inb 106-2/2-2/4-1/1	TZdEI 238	White	TZE-W POP STR 108 S5 195/198-2/2-3/3-3/3-5/5
TZEI 449	Yellow	(TZEI 11 x TZEI 8) S6 inb 107-6/6-4/7-1/1	TZdEI 272	White	TZE-W POP STR 108 S5 30/198-1/1-2/3-1/1-5/6
TZEI 456	Yellow	(TZEI 11 x TZEI 8) S6 inb 135-2/4-2/2-1/1	TZdEI 283	White	TZE-W POP STR 108 S5 34/198-1/2-1/3-1/2-2/3
TZEI 460	Yellow	(TZEI 11 x TZEI 8) S6 inb 142-3/3-5/5-1/1	TZdEI 275	White	TZE-W POP STR 108 S5 34/198-2/2-1/2-1/2-1/4
TZEI 461	Yellow	(TZEI 11 x TZEI 8) S6 inb 148-1/3-4/6-1/1	TZdEI 213	White	TZE-W POP STR 108 S5 40/198-1/1-3/3-2/2-5/5
TZEI 462	Yellow	(TZEI 11 x TZEI 8) S6 inb 148-1/3-6/6-1/1	TZdEI 192	White	TZE-W POP STR 108 S5 52/198-1/2-1/2-2/3-2/2
TZEI 464	Yellow	(TZEI 11 x TZEI 8) S6 inb 148-3/3-3/5-1/1	TZdEI 233	White	TZE-W POP STR 108 S5 56/198-1/2-2/4-1/2-2/3
TZEI 465	Yellow	(TZEI 11 x TZEI 8) S6 inb 148-3/3-4/5-1/1	TZdEI 280	White	TZE-W POP STR 108 S5 65/198-1/1-2/2-1/2-4/5
TZEI 467	Yellow	(TZEI 11 x TZEI 8) S6 inb 154-2/3-1/5-1/1	TZdEI 227	White	TZE-W POP STR 108 S5 69/198-1/1-1/2-1/2-2/5
TZEI 468	Yellow	(TZEI 11 x TZEI 8) S6 inb 154-2/3-3/5-1/1	TZdEI 228	White	TZE-W POP STR 108 S5 69/198-1/1-2/2-1/2-4/5
TZEI 470	Yellow	(TZEI 11 x TZEI 8) S6 inb 154-3/3-1/5-1/1	TZdEI 216	White	TZE-W POP STR 108 S5 86/198-1/1-2/2-2/2-2/6
TZEI 471	Yellow	(TZEI 11 x TZEI 8) S6 inb 154-3/3-3/5-1/1	TZEI 18	White	TZE-W Pop STR Co S6 Inbred 136-3-3
TZEI 472	Yellow	(TZEI 11 x TZEI 8) S6 inb 154-3/3-4/5-1/1	TZEI 19	White	TZE-W Pop STR Co S6 Inbred 143-3-3
TZEI 474	Yellow	(TZEI 11 x TZEI 8) S6 inb 170-1/3-2/6-1/1	TZEI 56	White	TZE-W Pop STR Co S6 Inbred 75-1-3
TZEI 475	Yellow	(TZEI 11 x TZEI 8) S6 inb 172-1/3-1/5-1/1	TZEI 35	White	TZE-W Pop STR Co S6 Inbred 7A
TZEI 476	Yellow	(TZEI 11 x TZEI 8) S6 inb 175-1/4-1/5-1/1	TZEI 31	White	TZE-W Pop x LD S6 Inbred 4
TZEI 485	Yellow	(TZEI 11 x TZEI 8) S6 inb 185-1/2-3/5-1/1	TZE1 3A	White	TZE-W Pop x 1368 STR S7 Inb. 4
TZEI 497	Yellow	(TZEI 11 x TZEI 8) S6 inb 201-1/2-6/6-1/1	TZE1 3B	White	TZE-W Pop x 1368 STR S7 Inb. 4
TZEI 520	Yellow	(TZEI 11 x TZEI 8) S6 inb 263-1/2-2/6-1/1	TZEI 83	White	TZE-W Pop x 1368 STR S7 Inb. 8
TZEI 443	Yellow	(TZEI 11 x TZEI 8) S6 inb 95-2/2-1/5-1/1	TZEI 5	White	TZE-W Pop x 1368 STR S7 Inb. 9
TZEI 13	Yellow	TZE Comp5-Y C6 S6 Inbred 12	TZdEI 52	Yellow	TZE-Y POP STR 106 S5 17/194-2/2-2/2-4/4-3/4
TZEI 16	Yellow	TZE Comp5-Y C6 S6 Inbred 31	TZdEI 51	Yellow	TZE-Y POP STR 106 S5 17/194-2/2-2/2-4/4-4/4
TZEI 17	Yellow	TZE Comp5-Y C6 S6 Inbred 35	TZdEI 46	Yellow	TZE-Y POP STR 106 S5 189/194-1/1-1/2-1/5-7/12

Table 3.1 Cont'd

Name	Endosperm Colour	Pedigree and selection history	Name	Endosperm colour	Pedigree and selection history
TZdEI 120	White	TZEE-W POP STR 104 S5 18/208-2/2-3/41/2-2/2	TZdEI 42	Yellow	TZE-Y POP STR 106 S5 189/194-1/1-1/22/5-3/5
TZdEI 124	White	TZEE-W POP STR 104 S5 83/208-1/1-2/23/4-1/3	TZdEI 68	Yellow	TZE-Y POP STR 106 S5 189/194-1/1-1/22/5-4/5
TZdEI 84	White	TZEE-W POP STR 104 S5 98/208-2/2-1/21/3-3/5	TZdEI 12	Yellow	TZE-Y POP STR 106 S5 2/194-1/1-1/2-1/23/4
TZdEI 71	White	TZEE-W POP STR 104 S5 98/208-2/2-2/21/2-1/2	TZEI 157	Yellow	TZE-Y Pop STR Co S6 Inbred 102-1-2
TZdEI 260	White	TZEE-W POP STR 108 S5 93/198-1/1-3/31/2-1/5	TZEI 127	Yellow	TZE-Y Pop STR Co S6 Inbred 10-3-4
TZdEI 41	Yellow	TZEE-Y POP STR 106 S5 121/194-1/1-1/12/3-1/2	TZEI 10	Yellow	TZE-Y Pop STR Co S6 Inbred 152
TZdEI 40	Yellow	TZEE-Y POP STR 106 S5 139/194-1/2-1/15/6-3/4	TZEI 129	Yellow	TZE-Y Pop STR Co S6 Inbred 16-1-3
TZdEI 16	Yellow	TZEE-Y POP STR 106 S5 17/194-2/2-2/24/4-3/3	TZEI 25	Yellow	TZE-Y Pop STR Co S6 Inbred 171-1-2
TZdEI 37	Yellow	TZEE-Y POP STR 106 S5 170/194-3/3-2/22/2-1/2	TZEI 135	Yellow	TZE-Y Pop STR Co S6 Inbred 17-2-3
TZdEI 24	Yellow	TZEE-Y POP STR 106 S5 189/194-1/1-1/22/5-2/6	TZEI 136	Yellow	TZE-Y Pop STR Co S6 Inbred 21-1-3
TZdEI 21	Yellow	TZEE-Y POP STR 106 S5 189/194-1/1-1/23/5-4/6	TZEI 124	Yellow	TZE-Y Pop STR Co S6 Inbred 3-1-3
TZdEI 48	Yellow	TZEE-Y POP STR 106 S5 189/194-1/1-1/24/5-9/9	TZEI 23	Yellow	TZE-Y Pop STR Co S6 Inbred 62-2-3
TZdEI 17	Yellow	TZEE-Y POP STR 106 S5 189/194-1/1-1/25/5-2/9	TZEI 8	Yellow	TZE-Y Pop STR Co S6 Inbred 62-3-3
TZdEI 65	Yellow	TZEE-Y POP STR 106 S5 189/194-1/1-1/25/5-9/9	TZEI 9	Yellow	TZE-Y Pop STR Co S6 Inbred 66
TZdEI 72	White	TZE-W POP STR 104 S5 1/208-1/1-3/3-3/34/9	TZEI 146	Yellow	TZE-Y Pop STR Co S7 Inbred 49-3-3

TZdEI 94	White	TZE-W POP STR 104 S5 127/208-1/3-2/33/3-1/2	TZEI 7	White	WEC STR S7 Inbred 12
TZdEI 153	White	TZE-W POP STR 104 S5 134/160-1/3	TZEI 26	White	WEC STR S8 Inbred 4

3.2.2 Experimental sites

Genotyping with the SSR markers was carried out at the Kirkhouse Trust funded biotechnology laboratory at CSIR-SARI main office located at Nyankpala in the Northern Region of Ghana. Genotyping of the inbred lines using SNP markers was carried out at CIMMYT, Mexico.

3.2.3 Molecular markers used

Thirty-one SSR markers (Appendix 1) and 51,009 SNP markers were screened in this study. The SSR markers were selected from earlier work by Senior *et al.* (1998).

3.2.4 DNA extraction and genotyping of the maize lines using SSRs and SNPs

Fresh leaf samples were collected from three-week old seedlings within each genotype and stored in a deep freezer at -80 ^{o}C. Prior to genomic DNA extraction, each sample was dried in a Labconco Freezone 2.5 L System lyophilizer (Marshall Scientific, USA) followed by grinding using Spex^{TM} Sample Prep 2010 Geno/Grinder (Thomas Scientific, USA). Total genomic DNA extraction was performed using the DArT protocol (www.diversityarrays.com/files/DArT_DNA_isolation.pdf). The quality and quantity of DNA in each sample was determined on 2% agarose gel followed by quantification using an ND-1000 Spectrophotometer (Nanodrop Technologies). For SSR genotyping, PCR amplification was carried out in a final volume of 10 µL reactions consisting of 5 µL of the 2X master mix (one Taq PCR master mix, VWR, UK), 3 µL of nuclease-free water, 1 µL of 5 µM forward and reverse primer and 1µL of 25 ng template DNA. The PCR was carried out using the ABI thermal cycler with the following conditions: initial denaturation at 94°C for 3 min, 35 cycles of denaturation at 94°C for 30 secs, annealing for 30 secs at a temperature depending on primer and extension at 72°C for 30 secs (Appendix 1). Amplified products were electrophoresed

using a 6% polyacrylamide gel on an hPAGE system (Cleaver Scientific, UK). Subsequently, the gel was stained with ethidium bromide for 30 min and visualized on UV transilluminator. For SNP genotyping, DNA samples were sent to Diversity Arrays Platform (Jaccoud *et al.*, 2001). Library construction, sequencing and SNP calling was performed at the Diversity Arrays Facility (Canberra, Australia).

3.2.5 Data analysis

Data on 94 inbred lines out of the 100 were subjected to statistical analysis as six of the inbred lines were inadvertently not genotyped using SNP markers. The polymorphic information content (PIC), major allele frequency, number of alleles, heterozygosity and gene diversity were estimated with the aid of PowerMarker V3.2.5 (Liu and Muse, 2005).

Single nucleotide polymorphism (SNP) markers with more than 20% of missing data, 20% of heterozygosity and the minor allele frequency lower than 0.05 were eliminated. Simple sequence repeat markers with more than 10% of missing data and 5% heterozygosity were excluded. The data cleaning resulted in 15 SSR and 15,047 SNP markers which were used for further analysis.

The data from the 15.047 SNP and 15 SSR polymorphic markers were subjected to population structure analysis using the admixture model-based clustering method and the software package STRUCTURE 2.3.4 (Zhang *et al.*, 2016). The best K for both types of markers was identified by inputting the data into the STRUCTURE HARVESTER software (XLSTAT, 2015; Adinsoft, 2010) utilizing the Evanno method (Evanno *et al*., 2005). For the SNP markers, the initial model was ran from 1 to 20 clusters (K) with 10 to 20 iterations for each K. Finally, the number of clusters was set at 10 with 10 alterations for each K. The results were obtained by running the data

against 10,000 MCMC and 10,000 burn-in as previously described by Liu and Muse (2005). For the SSR markers the model was ran again in order to estimate the best population structure by varying the number of clusters (K) from 1 to 12 with 10 iterations for each K. A burn-in period of 50,000 with an MCMC replications of 100,000 after each burn-in was used. Using the best K obtained, a final run was performed with a burn-in period of 100,000 and an MCMC of 200,000 to determine the final structure of the inbred lines. For both SNP and SSR markers, each genotype was assigned to a cluster at a 90% probability level, while genotypes with less than this value were assigned to an additional cluster designated as mixed cluster.

Following the determination of the number of clusters using STRUCTURE, the 15,047 SNPs and 15 SSRs data were analyzed using DARwin software (Zhang *et al.*, 2016) in separate sets, to generate the phylogenetic tree. The neighbor-joining method (NJ) under 30,000 bootstraps was used for both SNPs and SSRs. Genetic distance matrix was generated using the Jaccard similarity coefficient test (Jaccard *et al*., 1908) in the DARwin software (Perrier and Jacquemoud-Collet, 2006), which uses the formula d_{ij} = (b + c)/ (a+ (b +c)) where d_{ij} is the dissimilarity between units i and j, a is the number of variables where X_i is present and X_j is present, b is the number of variables where X_i is present and X_j is absent, c is the number of variables where X_i is absent and X_j is present. To generate the final phylogenetic tree the results obtained from DARwin were loaded into FigTree version 1.4.3 software (Rambaut, 2016).

3.3 Results

3.3.1 Genetic diversity revealed by SSR and SNP markers

The results of the summary statistics of the SNP markers are presented in Table 3.2. Heterozygosity averaged 0.07 and varied from 0.00 to 0.20. Gene diversity ranged from

0.01 to 0.50 with an average of 0.33. The major allele frequencies of the 15,047 markers averaged 0.84 with a range from 0.50 to 0.99. The PIC ranged from 0.01 to 0.38 with an average of 0.19. The highest and lowest minor allele frequency recorded were 0.50 and 0.01, respectively.

The results of the summary statistics of the SSR markers are also presented in Table 3.2. A total of 51 alleles were obtained using the 15 SSR markers with an average of 3 alleles per locus. The observed number of alleles ranged from 2 per locus for PHI109188 and NC130 to 5 per locus for PHI233376 and UMC1143. The major allele frequency of the SSRs ranged from 0.42 to 1.00 with a mean of 0.71. The highest major allele frequency was recorded by the markers PHI108411 and PHI423796. Gene diversity as depicted by the informative markers ranged from 0.05 to 0.72 with an average of 0.41. The highest gene diversity was recorded by the marker UMC1143 (0.72) and the lowest by PHI108411 (0.05) and PHI423796 (0.05). Heterozygosity ranged from 0.00 to 0.05 with a mean heterozygosity of 0.01. Twelve out of the 15 SSR markers had heterozygosity of 0.00. Polymorphic information content varied from 0.05 to 0.68 with a mean of 0.36. The highest PIC was recorded by the marker UMC1143. Four of the SSR markers used recorded PIC greater than 0.50 while 11 had values ranging between 0.05 and 0.48.

Table 3. 2 Summary statistics of the 15 SSRs and 15,047 SNP markers used to study the genetic diversity among 94 early maturing maize lines

Markers	Category	SSR	SNP
Alleles per locus	Min.	2	-
	Max.	5	-
	Mean	3.4	-
Major allele frequency	Min.	0.42	0.5
	Max.	0.78	0.99
	Mean	0.71	0.84
Heterozygosity	Min.	0	0
	Max.	0.05	0.2
	Mean	0.01	0.07
Gene Diversity	Min.	0.05	0.01
	Max.	0.72	0.5
	Mean	0.41	0.22
PIC	Min.	0.05	0.01
	Max.	0.68	0.38
	Mean	0.36	0.19

3.3.2 Genetic distance and population structure using SNP markers

The genetic distance between pairwise comparisons of the inbred lines varied from 0.06 to 0.65, and the overall average distance was 0.38. Majority (67.70%) of the genetic distances fell between 0.32 and 0.42 (Figure 3.1). The lowest genetic distance (0.06) was observed between inbred lines TZdEI 24 and TZdEI 68. Both inbred lines have the same descent and selection history (Table 3.1). The highest genetic distance (0.65) was observed between inbred lines TZEI 135 and TZEI 26. These inbred lines were derived from different source populations; TZEI 26 was extracted from WEC STR, which has white endosperm colour, while TZEI 135 was derived from TZE-Y Pop STR C_0, which has yellow endosperm colour (Table 3.1).

Based on 15,047 SNPs, population structure analysis revealed three distinct subpopulations in the 94 inbred lines (Figures 3.2A and 3.2B). The sub-population 1 consisted of 8.5% (8 lines) of the inbred lines, 20.2% (19 lines) were grouped into subpopulation 2 and 36.1% (34 lines) in sub-population 3. A 35.1% (33 lines) of the inbred lines had a probability of association less than 90%, hence were grouped into mixed populations (Appendix 2). The three sub-populations were separated mainly on the basis of the endosperm color, sub-populations 1 and 2 comprised only yellow endosperm maize inbred lines while majority of inbred lines (94%) in sub-population 3 consisted of white endosperm maize (Appendix 2). The results showed that subpopulation 1 contained only inbred lines derived from the source population TZEE-Y Pop STR 106 while about 97% of inbred lines in sub-population 2 were extracted from (TZEI 11 x TZEI 8). Sub-population 3 had the greatest diversity comprising six diverse source populations, namely TZE-W Pop STR 108, TZE-W Pop STR 104, (TZEI 1 x TZEI 2), TZE-W Pop x 1368 STR, WEC STR and TZE-W Pop STR Co. The expected heterozygosity among inbred lines within the three sub-populations ranged between 0.06 for sub-population 1 and 0.34 for sub-population 3 with an average of 0.19. Subpopulations 1, 2 and 3 had F_{ST} values of 0.83, 0.49 and 0.01, respectively. The highest allele frequency divergence of 0.15 was recorded between sub-populations 2 and 1, followed by sub-populations 3 and 1 with 0.11, while the least allele frequency divergence of 0.07 was recorded between sub-populations 2 and 3.

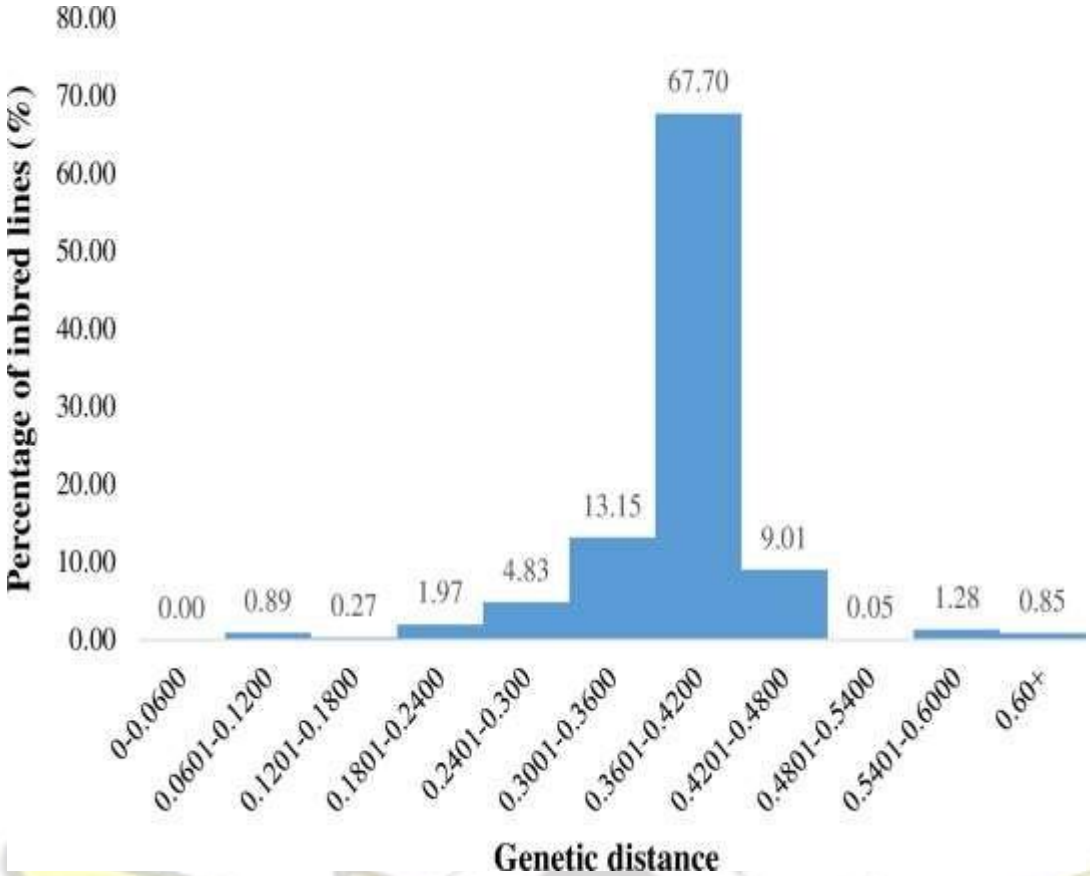

Figure 3. 1 Frequency distribution of pairwise genetic distances calculated based on Euclidean method for 94 tropical maize inbred lines genotyped with 15,047 SNP markers

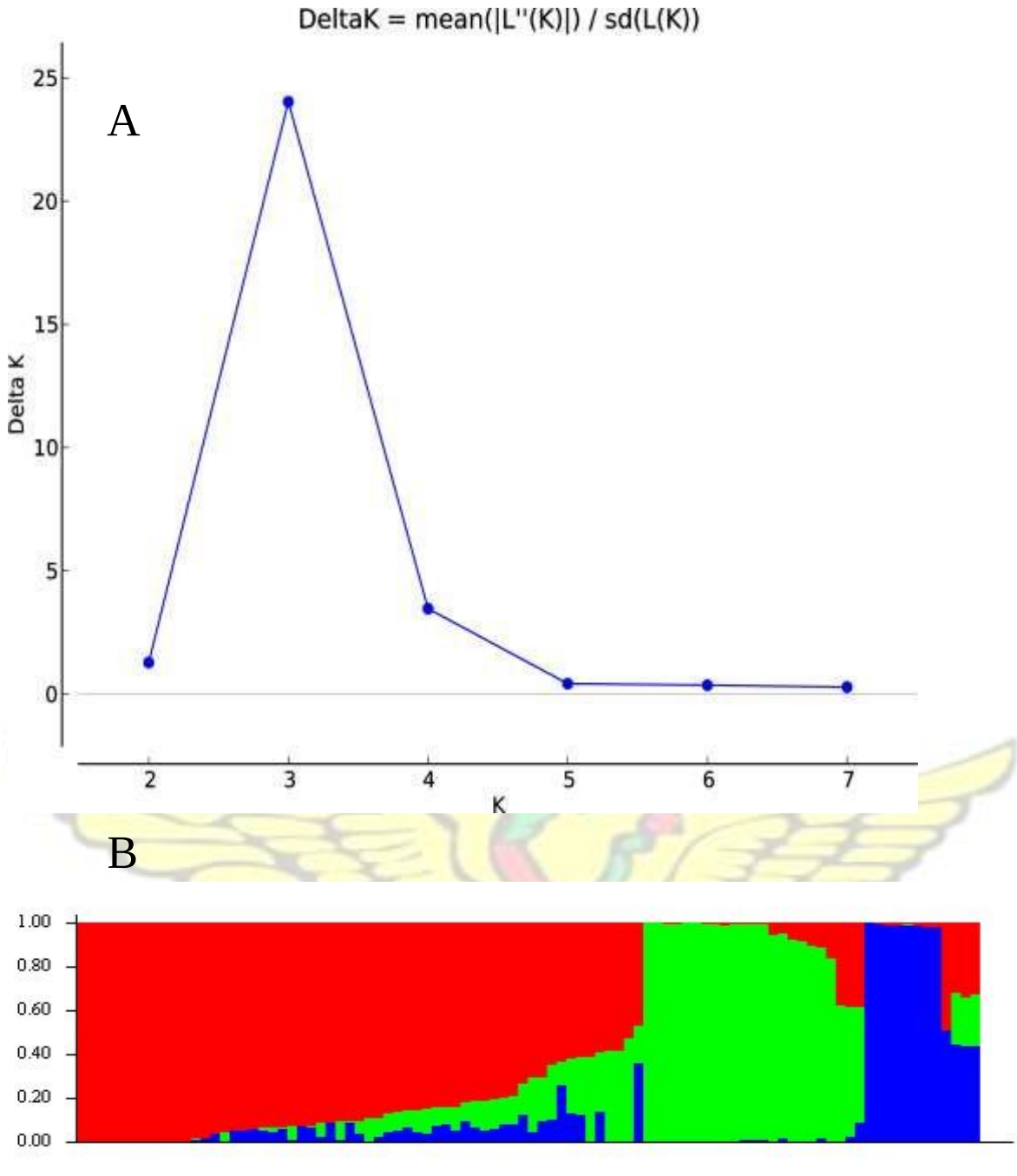

Figure 3. 2 The three sub-populations of the 94 tropical maize inbred lines using SNP markers. A: Best delta K estimation by Evanno method. B: Estimated population structure of 94 tropical maize inbred lines as revealed by 15,047 SNP markers for K = 3. Blue, green and red colour represents sub-population 1, 2, and 3, respectively

3.3.3 Cluster analysis by SNP markers

The results of the population structure analysis were confirmed by the phylogenetic tree which showed that the 94 inbred lines genotyped formed three clusters and each cluster was further partitioned into sub-clusters (Fig 3.3). In each cluster, inbred lines were coloured based on the results of the population structure analysis. Each colour represents specific sub-population such as lines coloured with blue, green, red and black corresponding to sub-population (SP) 1, 2, 3 and 4, respectively. The sub-population 4 represents the mixture of individuals with less than 90% association to any of the three sub-populations. The inbred lines were clustered based on their pedigree, selection history and endosperm colour (Appendix 2). Phylogenetic cluster 1 had a total of 14 inbred lines and represented a very clear sub-cluster of 8 lines (blue colour). This subcluster corresponded to sub-population 1 in population structure analysis (Figure 3.2B), with the remaining inbred lines considered as mixed genotypes. All 14 inbred lines were derived from TZE-Y Pop STR 106 and were characterized by yellow endosperm maize lines. The second cluster generated by the phylogenetic analysis included 32 inbred lines classified into several sub-clusters. However, it is clear that the grouping of 20 of the 32 maize inbred lines based on the phylogenetic analysis was similar to that based on the population structure analysis (SP2; green color) (Figure 3.2B and Appendix 2). Ninety-five percent of the inbred lines were extracted from the bi-parental cross TZEI 11 x TZEI 8 while one of the inbred lines was derived from TZE Comp5-Y C6. The remaining 17 inbred lines were derived from two source populations TZE-Y Pop STR Co and TZE Comp5-Y C_6 and were identified as mixed genotypes by structure analysis. The third and last cluster was the largest and most diverse among the three main clusters with 48 maize inbred lines. This cluster included inbred lines from

seven source populations, namely TZE-W P_{OP} STR 108, TZE-W P_{OP} STR 104, TZE-W Pop x 1368

STR, TZE-W Pop x LD, (TZEI 1 x TZEI 2), WEC STR and TZE-Y Pop STR Co (Table 3.1 and Appendix 2). All the inbred lines in this phylogenetic cluster belonged to subpopulation 3 (red colour) except 12 lines which were classified by the population analysis into the admixture group (Figure 3.3).

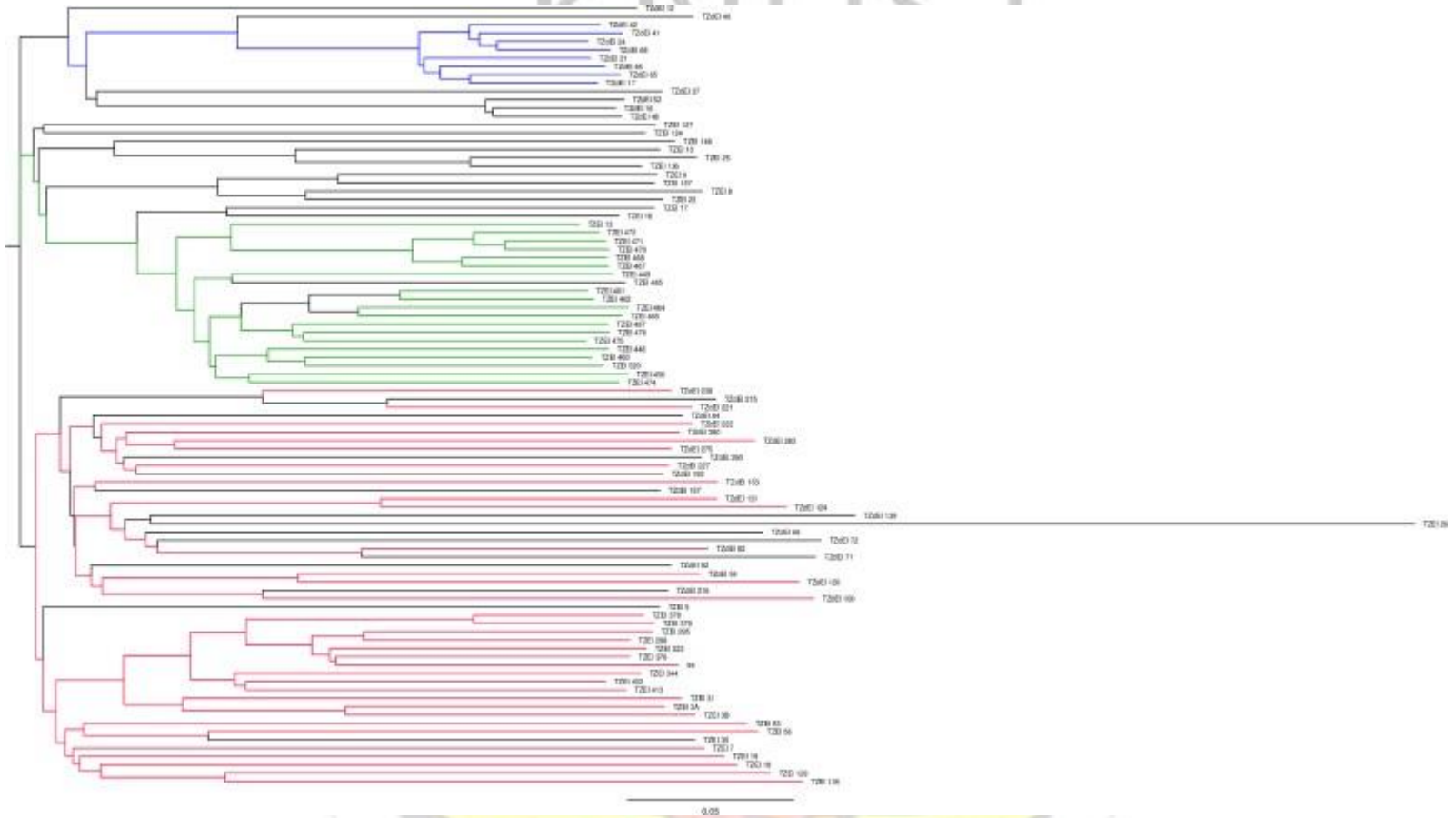
0.05

Figure 3. 3 Clustering of 94 tropical maize inbred lines based on 15,047 SNP markers. Clusters resulting from structure analysis are shown in blue, green and red colours. Mixed individuals that did not belong to any particular group at a 90% threshold are represented by the black colours

3.3.4 Diversity analysis using SSR markers

The genetic distance between pairwise comparisons of all the 94 inbred lines revealed by the SSRs ranged from 0.00 to 1.00, and the overall average distance was 0.71. About 66.96% of 4,371 pairwise comparisons fell between genetic distances of 0.60 and 0.90 (Figure 3.4). The genetic distance between TZEI 378 and TZEI 379 was the lowest (0.00) (Data not shown). Both TZEI 378 and TZEI 379 are sister lines with the pedigrees (TZEI 1 x TZEI 2) S_6 inb 190-1/9-1/3-1/1 and (TZEI 1 x TZEI 2) S_6 inb 190-1/9-2/3-1/1, respectively. The genetic distance between TZEI 16 and about 95.70% of the other inbred lines was 1. A complete lack of similarity was even recorded between TZEI 16, and TZEI 13 and TZEI 17, although, the three inbreds shared the same source population (TZE Comp5-Y C_6).

The 15 SSR markers grouped the 94 inbred lines into two major clusters that were divided into three sub-clusters (Figure 3.5). Sub-clusters 1 and 2 contained the highest number of inbred lines (43 and 46, respectively) while sub-cluster 3 contained only 5 inbred lines. The clustering of the inbred lines was based on pedigree and selection history of the inbred lines. All the three sub-clusters contained inbred lines extracted from diverse source populations (Table 3.1).

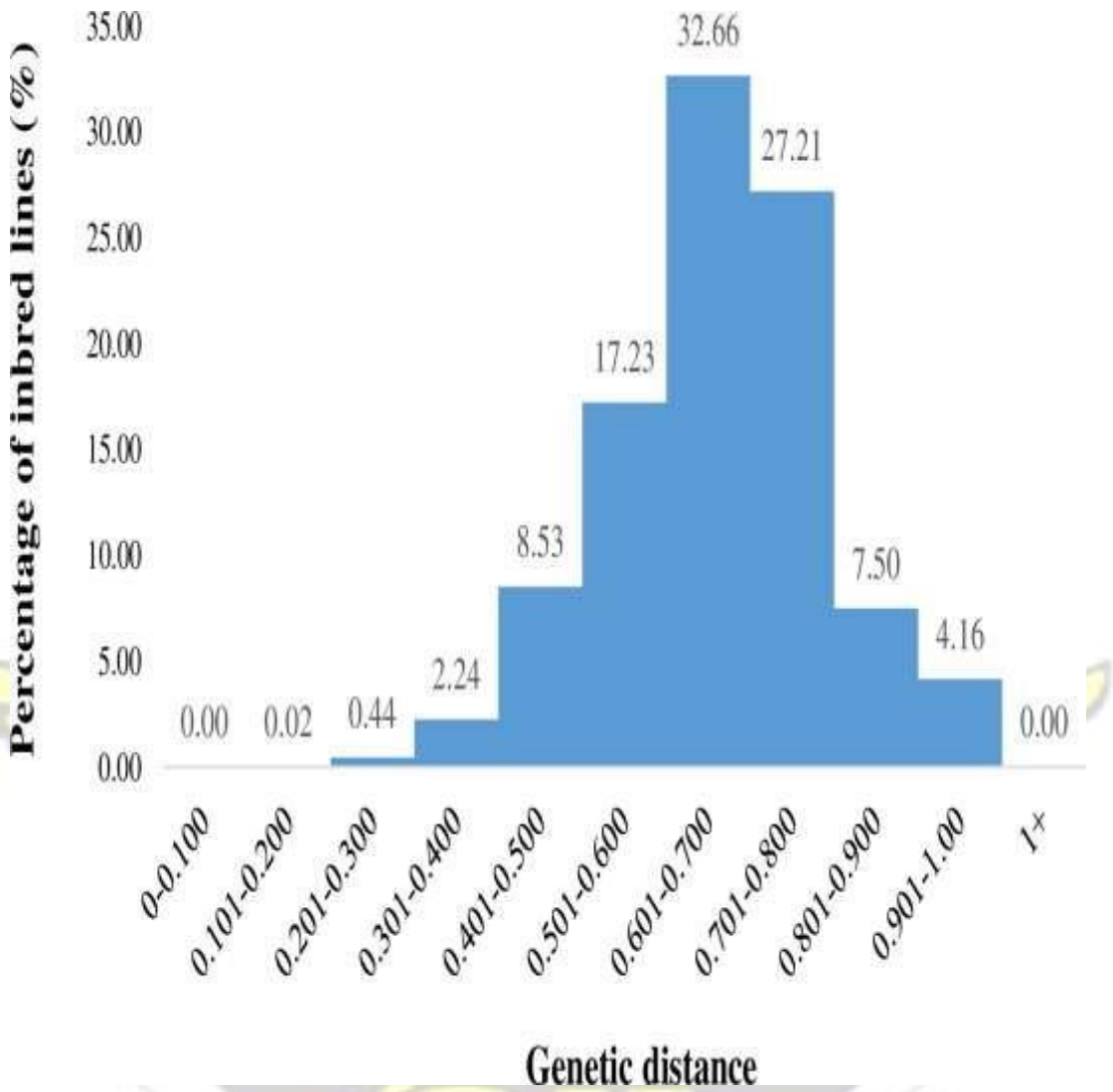

Figure 3. 4 Frequency distribution of pairwise genetic distances calculated based on Jaccard coefficient for 94 tropical maize inbred lines genotyped with 15 SSR markers

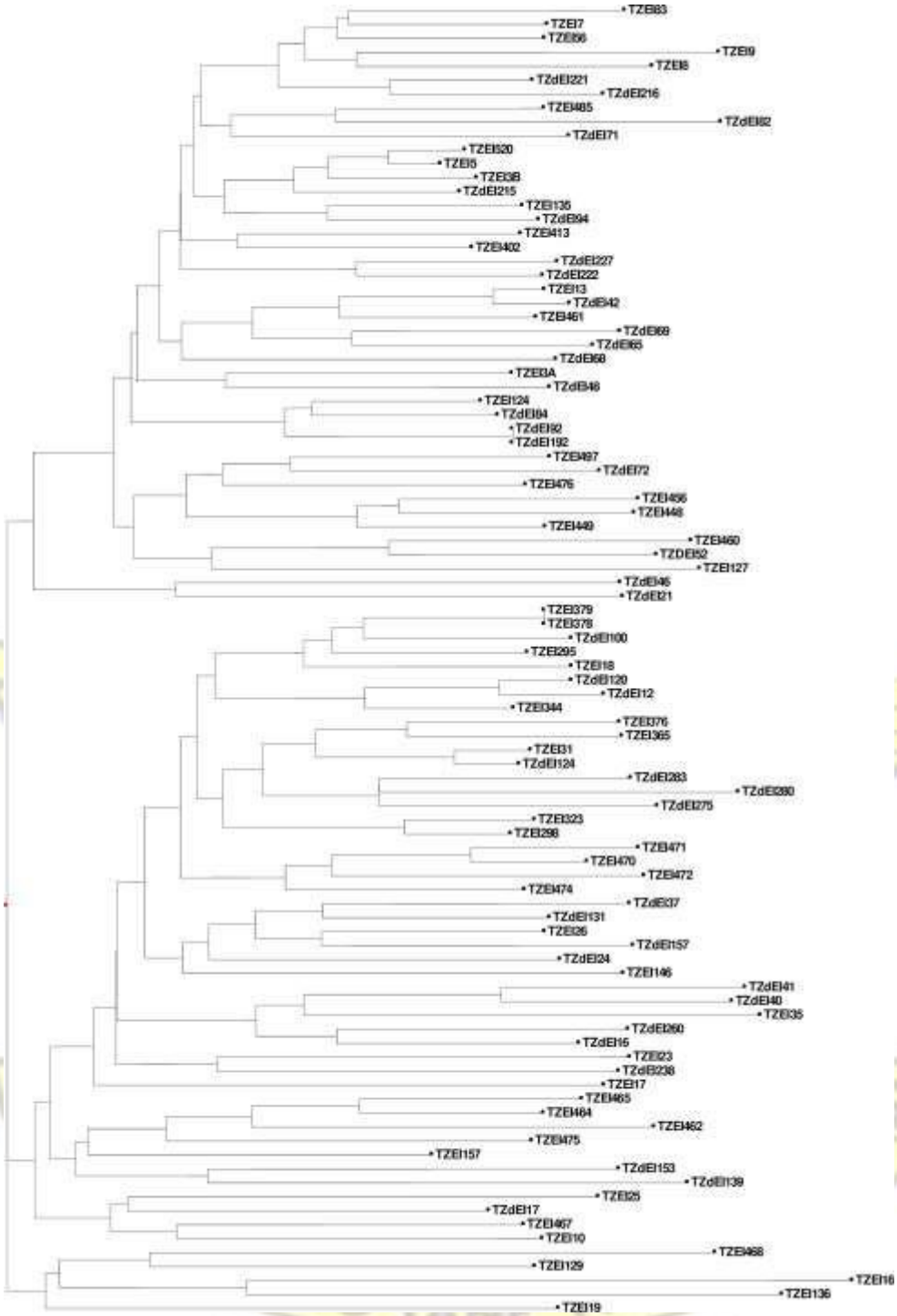

Figure 3. 5 Clustering of 94 tropical maize inbred lines based on 15 SSR markers

3.4 Discussion

Genetic diversity studies are very essential in the selection of individual genotypes among closely related groups for initiation of new breeding activities. It is particularly important that the genetic similarity or dissimilarity among inbred lines are established to facilitate the development of productive hybrids which are often a product of crosses involving inbred lines of opposing heterotic groups. Heterotic populations are also developed from inbred lines sharing common ancestry. New set of inbred lines are derived from the heterotic populations and the inbred lines are expected to combine well with inbred lines developed from other opposing heterotic populations. Genotyping has proved to be one of the reliable approaches of establishing such phylogenetic relationships among a set of inbred lines (Govindaraj *et al*., 2015). We studied the genetic diversity among 94 early maturing tropical maize inbred lines using 15,047 SNP and 15 SSR markers. It is important to note that due to the relatively low number of SSR to SNP markers used in this study, a comparison between the effectiveness of the two marker types in genetic diversity and population structure analyses was not done. In the present study, the mean number of alleles per locus of 3.40 detected by the SSRs was consistent with those of earlier reports in maize (Adeyemo *et al*., 2011, Makumbi *et al.,* 2015) but higher than 2.57 alleles per locus obtained by Akaogu *et al.* (2013) and Badu-Apraku *et al*. (2013). However, the mean alleles per locus was lower than 7.4 reported for maize lines by Xia *et al*. (2005). According to Reif *et al*. (2003), the total number of alleles in diversity studies is dependent on the sample size. The larger the population size the greater the frequency of the alleles in the population. This probably explains the differences in the number of alleles obtained in the present study. In the present study, the PIC average was of 0.19, a value found lower

than ones described by some researchers in maize (0.25–0.39) (Zhang *et al*., 2016, van Inghelandt *et al*., 2010, Wu *et al*., 2014) and sugar beet (0.28) (Simko *et al*., 2012), but similar to the results of Cruz *et al*. (2013) (0.21) in an oilseed crop Lesquerella, Bisen *et al.* (2014) in soybean, Ramakrishnan *et al.* (2016) in finger millet, and Oyekunle *et al*. (2015), Dao *et al.* (2014) and Senior *et al.* (2014) in maize. Approximately 49% of the SNPs presented a major allele frequency (MAF) of less than 0.1 (MAF<0.1) and 4.5% of the SNPs showed almost equal allele frequencies (MAF~0.5) for the two alternative alleles. Previously, it was shown in maize by using a set of 1,057 SNPs that IITA maize germplasm presented an average value of 0.218 and 0.202 for PIC and MAF values, respectively. Similar values were found for CIMMYT maize inbred lines (Dao *et al.*, 2014). The variation between our results and the findings of earlier researchers could be attributed to the differences in the composition of experimental materials, population size and number of markers involved in the studies (Xia *et al.*, 2005, Yan *et al.*, 2010).

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Genetic distance provides a measure of the degree of relatedness between individuals in a population (Garcia *et al*., 2004). Both the SSR and SNP markers revealed a wide genetic variability among the inbred lines with lower number of pairwise individuals with low genetic distances, suggesting that most of the inbred line used are unique and each of them has the potential to contribute new alleles to the breeding programme. The results of the cluster analysis based on SNPs appear to be more informative than the clustering from SSR markers. The SNP markers clustered the inbred lines based on their ancestry, selection history and endosperm colour. However, the clustering of some inbred lines was not based on shared ancestry, indicating that inbred lines extracted from the same source population

do not necessarily have the same selection history (Badu-Apraku *et al.*, 2006). The lack of association between clustering patterns and phenotypes, environmental adaptation, maturity and the heterotic groups has also been previously observed in CIMMYT maize germplasm (Xia *et al*., 2005, Warburton *et al*., 2002). Warburton *et al*. (2002) suggested that markers may be better indicators of relatedness of the inbred lines in cases where inbreds derived from the same source population are more different than those extracted from different source populations.

Population structure analysis is a process of inferring individual ancestry of inbred lines from genotypic information (Lawson and Falush, 2012). The smaller number of SSRs used in this study could not give a clear information on the population structure of the 94 inbred lines. This result corroborated the findings of Suteu *et al*. (2015) which indicated that for a precise assessment and assignment of inbred lines into respective clusters/populations as much as 70 informative markers should be used. The SNP markers revealed the presence of three sub-populations (K = 3) within the 94 inbred lines. Inbred lines with similar pedigree tended to cluster into the same group. The SNP markers clearly assigned inbred lines into heterotic groups based on the source populations, with individuals of the same endosperm colour and similar genetic background placed in the same sub-population. The grouping of inbred lines using SNP markers on the basis of similarity of pedigree and phenotype indicated that the SNP markers were very effective in assigning the inbred lines into homogenous groups. This result might have been influenced by the relatively larger number of SNPs used in the present study which would facilitate better interpretation of the results and inference about population structure (Xia *et al.,* 2004). The lower levels of heterozygosity observed among inbred lines within the three sub-populations suggested

that the SNPs were effective in forming homogeneous sub-populations. The very large FST values obtained for all three sub-populations and the moderate allele frequency divergence observed between sub-populations indicates that these inbred lines are fixed and can be classified into genetically distinct groups (heterotic groups). These characteristics make them a valuable resource for genetic studies in maize and association mapping where uniformity of inbred lines and genetic divergence are required. For future development of productive hybrids, crosses should be made between parent lines from different subpopulations, particularly between inbred lines in sub-populations 1 and 2.

CHAPTER FOUR

4.0 Evaluation of early maturing maize inbred lines for grain yield and superior agronomic performance under optimal, *Striga*-infested and low soil nitrogen environments

4.1 Introduction

Grain yield, the primary trait of interest of most breeding programs is a polygenic trait highly influenced by the environment, and thus has relatively low heritability estimates under stressful conditions. The combined use of grain yield and secondary traits improves selection efficiency in stressed environments, compared to measuring only grain yield (Edmeades *et al*., 1998). This is because under stress heritability of grain yield usually decreases, whereas heritability of some secondary traits remains high, while at the same time genetic correlation between grain yield and those secondary traits increases sharply (Bänziger and Lafitte 1997a; Edmeades *et al*., 2000). Breeders usually collect data on grain yield together with secondary traits to design multiple-trait selection indices to improve the chances of identifying superior stress resistant genotypes with improved grain yield.

The success of every hybrid development program relies heavily on the identification of inbred lines with superior performance in desirable traits. Although, inbred lines per se performance may not be good indicator of hyrid performance (Badu-Apraku and Fakorede, 2017), studies by Betrán *et al*. (2003) and Mesaka *et al*. (2011) have demonstrated that crosses between one or more low-N or drought tolerant inbred parents generated more productive hybrids under stress environments than those derived from two susceptible

parents. Earlier researchers have also concluded that selection on line per se basis is an effective method for improving combining value (Bohning, 1991). The objective of this study was to identify superior early maturing maize inbred lines based on multiple traits under optimal growing conditions, low soil nitrogen environments and artificial *Striga* infestation for hybrid development and population improvement.

4.2 Materials and methods

4.2.1 Genetic materials

The one hundred inbred lines described in Table 3.1 were used in this study.

4.2.2 Field evaluation

The inbred lines were evaluated in three different experiments in 2014 and 2015. In the first experiment, the inbred lines were evaluated for agronomic performance under artificial *Striga* infestation at Nyankpala (9^0 25' N and 0^0 58'E, 340 m ASL, 800 mm annual rainfall) in the Guinea savanna zone of Ghana. A 10 x 10 square lattice design with two replications were used. The experimental units were one-row plots, each 3 m long with an inter-row spacing of 0.75 m and intra-row spacing of 0.40 m. Each entry was infested with seeds of *Striga hermonthica*. About 5000 germinable *Striga* seeds were used in each hill for infestation. The *Striga* infestation method of IITA maize program was used (Kim, 1991). To promote germination and attachment of *Striga* to the roots of host plants under *Striga* infestation, fertilizer application was delayed until about 21 days after planting (DAP) (Kim, 1991) when 30 kg N ha^{-1}, 30 kg P ha^{-1}, and 30 kg K ha^{-1} was applied as 15–15–15 NPK. Weeds other than *Striga* were controlled manually.

In the second experiment, the inbred lines were evaluated under low-N (30 kg N ha^{-1}) environment at Kwadaso (6° 42' 0" N and 1° 39' 0" W, 251 m ASL, 1500 mm annual rainfall) in the Forest zone of Ghana. The experimental field used for the low-N evaluation had already been depleted of N by continuously planting maize and removing the biomass after each harvest for several seasons. Soil samples were taken before planting for soil analysis to determine the N content of the field. Soil analyses were done at the soil analytical laboratory at the Kwame Nkrumah University of Science and Technology,

Kumasi using the Kjeldahl digestion and colorimetric method (Bremner and Mulvaney, 1982). The same experimental design and plot size described in the first experiment was used in the second experiment. Based on the results of the soil test (Appendix 3), fertilizers were applied to bring the total available N to 30 kg ha^{-1} for low-N environments. The N fertilizer was applied at 2 WAP, immediately after thinning. Also, single superphosphate (P_2O_5) and muriate of potash (K_2O) were applied to the low-N plots at the rate of 60 kg ha^{1}. The experiments were kept weed free with the application of atrazine (1-chloro-3ethylamino-5-isopropylamino-2-4-6-triazine) as pre-emergence herbicide at 5 L ha^{-1} and subsequently by hand weeding when necessary.

The inbred lines were also evaluated under optimal growing conditions [High-N (90 kg N ha^{-1}) and *Striga*-free environments] in the third experiment at Nyankpala and Kwadaso. The experimental design and plot size were similar to that used in the first and second experiments. A compound fertilizer was applied at the rate of 60 kg ha^{-1} N, P and K at 2 WAP immediately after thinning. An additional 30 kg N ha^{-1} was top-dressed 4 weeks later.

Weed control method used in the third experiment were the same as those used in the second experiment.

4.2.3 Data Collection

Data were recorded on low-N, optimal and *Striga*-infested plots at all sites for the following traits:

i. Days to anthesis (DA): The number of days from planting to the time when 50% of plants had tassels shedding pollen.

ii. Days to silking (DYSK): The number of days from planting to the time when 50% of plants had emerged silks.

iii. Ear height (EH): The average height of the ear in centimeters (cm) from ground level to the node bearing the uppermost ear.

iv. Plant height (PH): The average height of plants in centimeters (cm) from the base of the plant to the node bearing the flag leaf.

v. Plant stand (PS): Total number of plants per plot obtained soon after thinning vi. Plants per plot (PHARV): Total number of plants harvested per plot.

vii. Ears per plot (EHARV): Total number of ears harvested per plot.

viii. Husk cover (HC): Husk cover was rated on a scale of 1-5, where 1 = husks tightly arranged and extended beyond the ear tip and 5 = ear tips exposed.

ix. Moisture: Grain moisture taken by moisture tester at harvest in percentage.

x. Plant aspect (PASP): Plant aspect was rated on a scale of 1–5, where 1 = excellent overall phenotypic appeal, 2 = very good overall phenotypic appeal, 3 =good overall phenotypic appeal, 4= poor overall phenotypic appeal and 5 = very poor overall phenotypic appeal. xi. Ear aspect (EASP): Ear aspect was scored on a scale of 1–5, where 1=excellent with no

disease/insect damage, large cobs, uniform ears and fully filled grains, 2 =good with no disease/insect damage and fully filled grains, one or two irregularity in cob size, 3= mild insect damage, no disease, fully filled grains, one or two irregularity in cob size, 4= severe disease/insect damage, scanty grain filling, few ears, non-uniformity of cobs and 5= only one or no ears.

xii. Root lodging (RL): Number of plants that fell from the root. The number of plants that are root-lodged were scored on a scale of 1-5, where 1= no lodging of plants; 2=more than 20% of plants lodged; 3= more than 40% of plants lodged; 4=more than 60% of plants lodged and 5=more than 80% of plants lodged.

xiii. Stalk lodging (SL): Number of plants with broken stalk below the ear or the stalk bending more than 45^0 from the upright position. The number of plants that are stalk-lodged were scored on a scale of 1-5, where 1= no lodging of plants; 2=more than 20% of plants lodged; 3= more than 40% of plants lodged; 4=more than 60% of plants lodged and 5=more than 80% of plants lodged.

xiv. Field weight (FWT): The weight of cobs per plot measured in kilograms.

xv. Grain yield (GYLD): Grain yield was calculated in kilogram per hectare corrected to 15% moisture. In the low-N experiment, harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield was adjusted to 15% moisture and computed from the shelled grain weight, while grain yield was calculated based on field weight in the *Striga*-infested and optimal experiments. A shelling percentage of 80% was assumed for inbred lines per plot and grain yield (obtained from ear weight and converted to kg ha^{-1}) was adjusted to 15% moisture content.

xvi. Anthesis-silking interval (ASI): Calculated as the difference between days to anthesis and days to silking.

xvii. Ears per plant (EPP): Computed by dividing the total number of ears harvested per plot by the total number of plants harvested per plot.

In addition to the above traits, the following traits were also measured under either *Striga*infested or low-N environments:

i. Stay green characteristic (leaf death score (LD): Stay green characteristics (Stay green) was scored for low-N plots at 70 DAP on a scale of 1–9, where 1 = 0-10% dead leaf area, 2 = 10-20% dead leaf area, 3 = 20-30% dead leaf area, 4 = 30-40% dead leaf, 5 = 50-60% dead leaf area, 6 = 60-70% dead leaf area, 7 = 70-80% dead leaf area, 8 = 80-90% dead leaf area and 9 = 90-100% dead leaf area.

ii. *Striga* emergence count 1 (STRCO1): The number of emerged *Striga* plants count per plot at 8 WAP for plots under *Striga* infestation.

iii. *Striga* emergence count 2 (STRCO2): The number of emerged *Striga* plant count per plot at 10 WAP for *Striga*-infested plots.

iv. *Striga* damage syndrome rating 1 (STRRAT1): *Striga* damage syndrome was rated per plot for *Striga* infested plots on a scale of 1–9, where 1= Normal plant growth, no visible symptoms, 2=Small and vague purplish-brown leaf blotches visible, 3= Mild leaf blotching with some purplish-brown necrotic spots, 4= Extensive blotching and mild wilting. Slight but noticeable stunting and reduction in ear and tassel size, 5=Extensive leaf blotching, wilting and some scorching, moderate stunting; ear and tassel size reduction.6=Extensive leaf scorching with mostly grey necrotic spots, some stunting and reduction in stem

diameter, ear size and tassel size, 7=Extensive leaf scorching, with grey necrotic spots, and leaf wilting and rolling, severe stunting and reduction in stem diameter, ear size and tassel size, often causing stalk lodging, brittleness and husk opening at the late growing stage, 8=Extensive leaf scorching with extensive grey necrotic spots, conspicuous stunting, leaf wilting, rolling, severe stalk lodging and brittleness, reduction in stem diameter, ear size and tassel size, and 9= Complete scorching of all leaves, causing premature death or collapse of host plant and no ear formation.

v. *Striga* damage syndrome rating 2 (STRRAT2): *Striga* damage syndrome was rated per plot for *Striga* infested plots on a scale of 1–9 as described for *Striga* damage syndrome rating 1.

4.2.4 Data analysis

4.2.4.1 Analysis of variance

Separate analyses of variance (ANOVA) were performed on all collected data under optimal, low-N and *Striga* infested environments using the general linear model procedure (PROC GLM) in Statistical Analysis System (SAS) (SAS Institute, 2008) using a random statement with test option. *Striga* emergence counts were transformed using natural logarithm transformation (LN (count+1)) before analysis. Subsequently, combined ANOVA across locations and years were performed for DA, DYSK, EASP, EH, PH, PS, PHARV, EHARV, ER, HC, PASP, RL, SL, GYLD, ASI and EPP. Each combination of location by year was regarded as a test environment. In the combined ANOVA, the environments, replicates within environment, incomplete blocks within replicates × environment interaction were regarded as random factors. The entries were considered as fixed factor.

4.2.4.2 Multiple-trait selection index for low-N tolerance and *Striga* resistance

The IITA maize program's base index for identifying genotypes with low-N tolerance (Menkir and Akintunde, (2001) and *Striga* resistant/tolerant (MIP 1996) genotypes were used. The selection indices described below were used to characterize and separately select inbred lines with tolerance and/or resistance to *Striga* and low-N environments. The base index used for selection of *Striga* resistance/tolerance (BI_{STR}) was computed as follows:

$$BI_{STR} = [(2\ x\ GYLD) + EPP - (STRRAT1 + STRRAT2) - 0.5(STRCO1 + STRCO2)]$$

Where GYLD is the mean grain yield of *Striga*-infested plots, EPP is the number of ears per plant in *Striga*-infested plots, STRRAT1 and STRRAT2 are *Striga* damage syndrome rating at 8 and 10 WAP, respectively and STRCO1 and STRCO2 are the number of emerged *Striga* plants at 8 and 10 WAP, respectively. The base index for selection of low-N tolerant inbred lines (BI_{LN}) was computed as follows:

$$BI_{LN} = [(2\ x\ GYLD) + EPP - ASI - PASP - EASP - LD]$$

Where GYLD is the mean grain yield of low-N plots, PASP is the plant aspect, EASP is the ear aspect, EPP is the number of ears per plant, ASI is anthesis-silking interval, and LD is stay green characteristic. A base index for multiple stress tolerance (MI) proposed by Badu-Apraku *et al*. (2016) was used to select inbred lines with multiple stress tolerance to low-N and *Striga* infestation. The multiple stress tolerance base index was computed as follows:

$$MI = (2\ x\ GYLD) + EPP - EASP - PASP - LD - STRRAT1 - STRRAT2$$

$$- (0.5\ x\ STRCO1) - (0.5\ x\ STRCO2)$$

Where GYLD is grain yield, EPP is number of ears per plant, EASP is ear aspect and PASP is plant aspect across *Striga* infestation, low-N and stress-free environments; LD is stay green characteristic under low-N environment; STRRAT1 and STRRAT2 and STRCO1 and STRCO2 are *Striga* damage at 8 and 10 WAP and number of emerged *Striga* plants at 8 and 10 WAP across *Striga*-infested environments. Under *Striga* infestation, low-N and optimal growing conditions, each trait was standardized, with a mean of zero and standard deviation of 1 to minimize the effects of different scales. For each test environment, therefore, a positive value indicated tolerance while a negative value indicated susceptibility of the inbred line to the respective stress. For selection across environments, a positive MI value was considered an indication of combined tolerance/resistance to lowN and *Striga infestation*, while negative values indicated susceptibility.

4.2.4.3 Path coefficient analysis of grain yield and yield components

The entry means of all traits measured under each of the three research conditions (optimal, striga-infested and low-N environments) were standardized and used for phenotypic correlation and multiple regression analyses in Microsoft office Excel (2013 version). In the multiple regression analysis, traits that caused high multicollinearity effects were removed step by step from the analysis. Outputs from the correlation and regression analyses were used for path coefficient analysis following procedures described by

Akintunde (2012) to calculate the direct and indirect effects of the other traits on grain yield.

4.2.4.4 Genotype by trait and trait association by environment analyses

The GGE biplot pattern explorer (Yan, 2001) was used for trait association and trait profile analyses. The model for Genotype by Trait (GT) biplot (Yan and Rajcan, 2002) used is presented below:

$$\frac{(Y_{ij} - \mu - \beta_j)}{d_j} = \lambda_1 g_{i1} e_{1j} + \lambda_2 g_{i2} e_{2j} + \varepsilon_{ij}$$

Where Y_{ij} is the genetic value of the combination between inbred i and trait j; μ is the mean of all combinations involving trait j; β_j is the main effect of trait j; λ_1 and λ_2 are the singular values for PC1 and PC2; g_{i1} and g_{i2} are the PC1 and PC2 eigenvectors, respectively, for inbred I; e_{1j} and e_{2j} are the PC1 and PC2 eigenvectors, respectively, for trait j: d_j is the phenotypic standard deviation (with mean of zero and standard deviation of 1); and ε_{ij} is the residual of the model associated with the combination of Inbred i and trait j. The data were not transformed ('Transform = 0'), but were standard deviation-standardized ('Scale = 1'), and trait-centered ('centering = 2'). Therefore, the outputs are appropriate for visualizing the relationships among genotypes and traits.

Trait Association by Environment (ABE) biplot analysis (Yan and Tinker, 2005 and Yan *et al.*, 2007b) was used to display associations between grain yield as a target trait and days to anthesis, days to silking, plant height, ears per plant, ear aspect, and plants and ears harvested per plot as explanatory traits. The analysis was based on procedures by Yan and

Tinker (2005a) and Yan *et al.* (2007b). The "Multi-Trait Decision Maker-Against Toplines" module, which combines independent selection and culling, and index selection in one selection platform was used to identify lines adpted to all the three research conditions. It was specified that an inbred line having a level lower than 70% of the top inbred line for any trait should be discarded ("independent culling"), and a genotype with a level higher than 95% of the best inbred line for any trait should be retained ("independent selection"). Independent selection takes the priority, independent culling the second, and index selection the last. The following traits and weights were used: days to silking (-0.7), days to anthesis (-0.7), plants per plot (0.5), ears per plot (0.7) and grain yield (1.0).

4.3 Results

4.3.1 Analysis of variance of yield and other traits of the inbred lines under optimal, *Striga*-infested and low-N environments, and across test environments

Analysis of variance across the optimal growing environments (Table 4.1) showed significant genotypic differences among the inbred lines for grain yield, days anthesis and silking, ears per plant, ear aspect, plant and ear heights (Table 4.2). Mean square value for environment was significant for grain yield, days to silking, plant height and ear height. Genotype x environment (G x E) interaction was significant for grain yield, plant aspect, days to anthesis, days to silking and ear aspect (Table 4.2). Results of analysis of variance showed significant ($P \leq 0.001$) genotypic mean squares for grain yield, ears per plant, ear aspect, plant height and *Striga* damage syndrome ratings at 8 and 10 WAP under artificial *Striga* infestation (Table 4.3). The mean square for environment was significant ($P \leq 0.001$) for ear height, plant height, root lodging and stalk lodging under Striga-infested environments. Significant differences ($P \leq 0.001$) were detected among the inbred lines for

grain yield, days to anthesis, days to silking, ears per plant, ear aspect, ear height and stay green characteristic across the low-N environments (Table 4.4). There were significant differences among environments for grain yield, ear height, plant height and root lodging in low-N environments. Combined ANOVA across optimal growing conditions, *Striga*infested and low-N environments showed significant differences ($P \leq 0.001$) among genotypes for days to anthesis, days to silking, plant height, ear aspect, ear height and ears per plant. Differences among environments were also significant ($P \leq 0.001$) for grain yield, days to anthesis, days to silking, plant height, ear aspect, ear height, ears per plant, root lodging and stalk lodging (Table 4.6). Genotype x environment interaction was extremely significant for grain yield, days to anthesis, days to silking, plant height , ear aspect and ears per plant (Table 4.5).

Table 4. 1 Description of test environments used in the study

Test environment	Research condition	Year	Location
1	Optimal	2015	Kwadaso
2	Optimal	2015	Nyankpala
3	*Striga*-infested	2014	Nyankpala
4	*Striga*-infested	2015	Nyankpala
5	Low nitrogen	2014	Kwadaso
6	Low nitrogen	2015	Kwadaso

Table 4. 2 Mean squares of grain yield and agronomic traits of 100 early maturing maize inbred lines across optimal growing conditions at Kwadaso and Nyankpala in 2015

Source of variation	D.F.	Grain yield	Plant aspect	Days to anthesis	Days to silking	Ears per plant	Ear aspect	Plant height	Ear height
Environment (E)	1	17487260.80***	0.01ns	2.85ns	12.07 *	0.03ns	0.00 ns	14732.05***	6993.08***
Replication (E)	2	842443.90ns	0.03 **	29.98 ns	33.15 ***	0.00 ns	0.01 ns	1001.30 ns	5.85 ns
Block (REP x E)	36	1193805.00*	0.08 *	4.25 ns	4.70 **	0.01 ns	0.06 ns	312.95 ns	88.48 ns
Genotype (G)	99	1606821.40***	0.12 ns	7.43***	12.13***	0.02*	0.17 **	915.37***	154.43***
G x E	99	1988174.30***	0.13**	3.42 **	4.09 ***	0.01ns	0.17 **	347.78ns	76.67 ns
Error	181	684803.80	0.08	2.33	2.31	0.01	0.11	277.26	67.99
CV (%)		19.90	10.03	3.09	3.04	12.39	12.04	12.78	14.10

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns = non- significant, respectively, REP = replication

Table 4. 3 Mean squares of grain yield and agronomic traits of 100 early maturing maize inbred lines across artificial *Striga* infestation at Nyankpala in 2014 and 2015

Source of variation	D.F.	Grain yield	Ears per plant	Ear aspect	Ear height	Plant height	Root lodging	Stalk lodging
Environment (E)	1	43747.90^{ns}	0.01^{ns}	0.64^{ns}	2809.00***	99288.01***	243.36***	174.24***
Replication (E)	2	7983711.20**	0.03 ^{ns}	1.03^{ns}	1.50 ^{ns}	82.84^{ns}	2.29 **	5.68***
Block (REP x E)	36	2717718.50***	0.02 ^{ns}	0.27^{ns}	174.54 ^{ns}	853.84*	0.22 ^{ns}	0.41 ^{ns}
Genotype (G)	99	1525472.30***	0.07***	2.09***	138.74 ^{ns}	700.02***	0.21 ^{ns}	0.34 ^{ns}
G x E	99	894555.90 ^{ns}	0.02 ^{ns}	0.60^{ns}	95.96 ^{ns}	333.46 ^{ns}	0.24 ^{ns}	0.40 ^{ns}
Error	190	992396.80	0.02	0.57	115.96	420.74	0.21	0.37
CV (%)		35.60	16.27	15.01	28.59	18.35	36.10	48.04

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns = non- significant, respectively, REP = replication

Table 4.3 (cont'd)

Source of variation	D.F.	*Striga* emergence count	*Striga* damage syndrome rating

		8 WAP	10 WAP	8 WAP	10 WAP
Environment (E)	1	102.01 ^{ns}	200.22 ^{ns}	2.10 ^{ns}	1.32 ^{ns}
Replication (E)	2	1541.28***	4323.19***	2.42 ^{ns}	1.98 ^{ns}
Block (REP x E)	36	54.66 ^{ns}	87.62 ^{ns}	1.03 ^{ns}	0.84 ^{ns}
Genotype (G)	99	60.34 ^{ns}	123.85 ^{ns}	3.51***	2.55***
G x E	99	55.22 ^{ns}	121.31 ^{ns}	1.12 ^{ns}	0.92 ^{ns}
Error	190	64.08	116.05	1.14	0.94
CV (%)		68.26	59.00	25.45	20.28

*** $P \leq 0.001$, ns = non- significant, respectively, REP = replication

Table 4. 4 Mean squares of grain yield and agronomic traits of 100 early maturing maize inbred lines evaluated across low soil nitrogen at Kwadaso in 2014 and 2015

Source of variation	D.F.	Grain yield	Days to anthesis	Days to silking	Ears per plant	Ear aspect	Ear height	Plant height	Root lodging	Stay green
Environment (E)	1	89070905.50***	1.10 ns	3.42 ns	0.01 ns	0.56 ns	1781.34 **	12786.65***	14.1***	0.30 ns
Replication (E)	2	20130997.30***	3.22 ns	1.59 ns	0.00 ns	4.36 *	2903.14***	4421.04 **	0.12 ns	0.65 ns
Block (REP x E)	36	2020436.40 *	3.40 ns	3.66 ns	0.01 ns	1.22 *	153.83 ns	305.20 ns	0.33 ns	0.57 ns
Genotype (G)	99	1595863.00 *	9.46***	10.50***	0.01 **	1.15 **	176.74 *	720.76 ns	0.26 ns	1.22***
G x E	99	921225.90 ns	3.72 ns	3.78 ns	0.01 ns	0.51 ns	84.07 ns	388.19 ns	0.20 ns	0.46 ns
Error	178	1154240.70	3.78	3.96	0.01	0.72	130.62	565.96	0.24	0.54
CV (%)		50.69	3.25	3.22	11.28	17.37	21.89	19.36	38.83	13.83

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns = non- significant, respectively, Rep = replication

Table 4. 5 Mean squares of grain yield and agronomic traits of early maturing maize lines evaluated across *Striga*infested, low soil nitrogen and optimal growing environments in 2014 and 2015

Source of Variation	D.F.	Grain yield	Days to anthesis	Days to silking	Plant height	Ear aspect
Environment (E)	5	321843225.00***	4445.58***	5634.280***	38946.90***	264.29***
Replication (REP)	1	14095825.00***	14.23 *	9.866 ns	590.67 ns	2.94 **
Block (Rep)	18	1981338.00 **	5.97 **	7.908 **	742.54 *	0.80 *
Genotype (G)	99	1676682.00 ***	10.95***	16.668***	1363.70***	1.17***
G x E	495	1463220.00***	6.75***	8.180***	395.24 ns	0.69***
Error	578	1004312.00	2.93	3.572	416.87	0.47
CV (%)		38.91	3.13	3.388	16.79	16.21

* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, ns = non- significant, respectively, REP = replication

Table 4.5 Cont'd

Source of variation	D.F.	Ear height	Ears per plant	Root lodging	Stalk lodging

Environment (E)	5	20503.31***	0.56***	59.38***	69.69***
Replication (E)	6	989.97**	0.01 ns	1.13 ns	1.39 ns
Block (REP x E)	108	214.57**	0.0 ns	0.18 ns	0.30 ns
Genotype (G)	99	229.22***	0.03***	0.24 ns	0.28 ns
G x E	495	100.09	0.02***	0.18 ns	0.39 ns
Error	578	106.53	0.02	0.18	0.36
CV (%)		20.87	13.28	40.03	46.12

** P ≤ 0.01, *** P ≤ 0.001, ns = non- significant, respectively, REP = replication

4.3.2 Mean performance of the inbred lines under optimal, *Striga*-infested and low-N environments, and across test environments

Averaged across test environments, overall mean grain yield of the inbred lines was 768 kg ha^{-1} (Appendix 4). Mean grain yield was higher under optimal growing conditions (1076 kg ha^{-1}) followed by low-N (837 kg ha^{-1}) and lowest under *Striga* infestation (686 kg ha^{-1}) (Appendix 4). Under *Striga* infestation and low-N environments, anthesis-silking interval was wider and the number of root lodged plants was greater (Figures 4.1 and 4.2). Plant height and ears per plant of the inbred lines reduced under *Striga* infestation and low-N with a more pronounced reduction in plant height under low-N. The longest day to silking was recorded under low-N, while the poorest ear aspect was recorded under *Striga* infestation (Figure 4.2). Using the multiple-trait indices for the selection of *Striga* resistant/tolerant, low-N tolerant and multiple-stress tolerant inbred lines, forty-eight of the 100 inbred lines had positive base index values under low-N environments (0.2 to 17.0), whereas forty-nine of them had positive base index values under *Striga* infestation (0.1 to 7.5) and across environments (9.5 to 0.2) (Appendix 4).

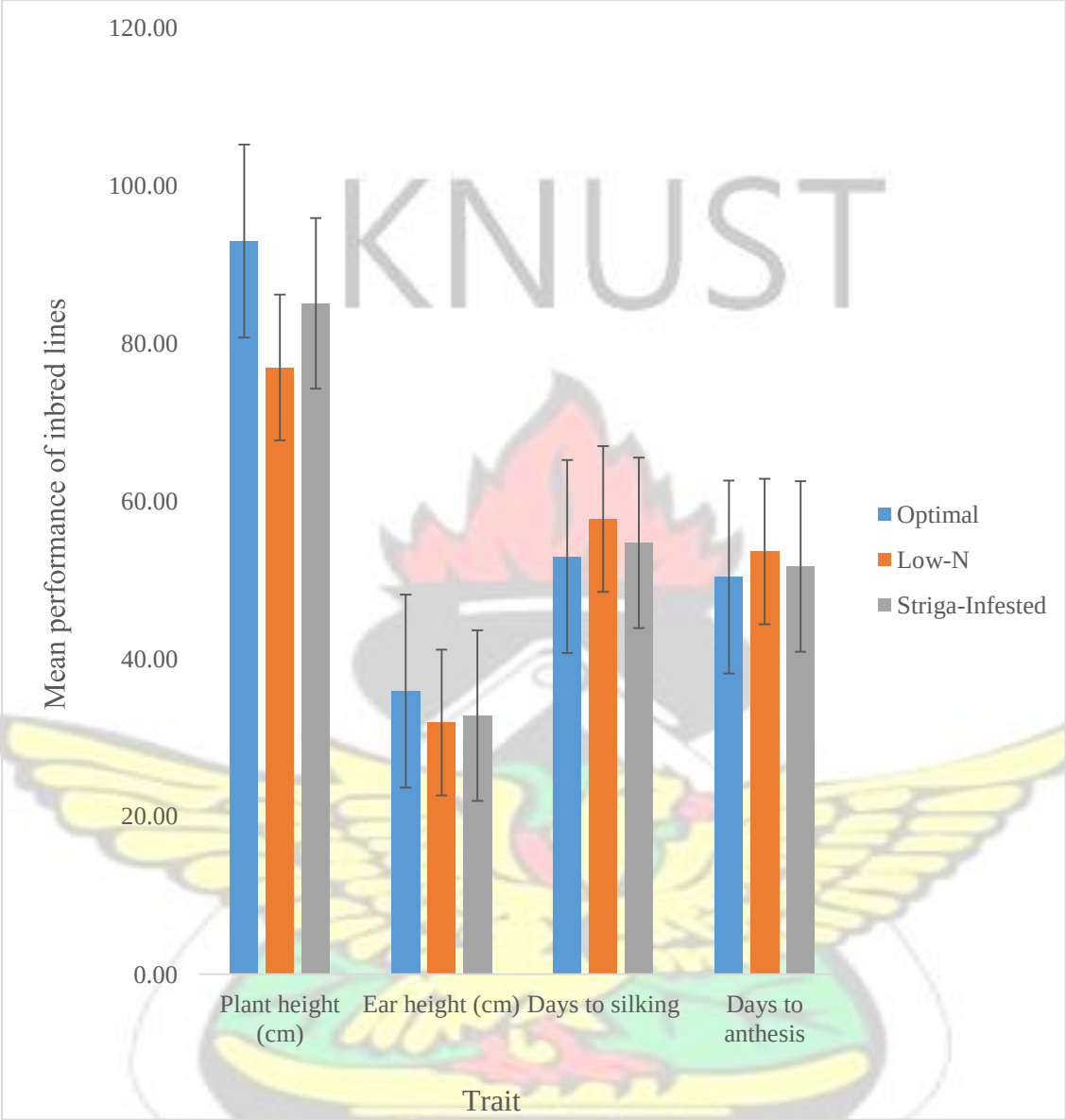

Figure 4. 1 Mean plant height, ear height, days to silking and days to anthesis of the 100 inbred lines evaluated across optimal growing conditions, *Striga*-infested and low-N environments

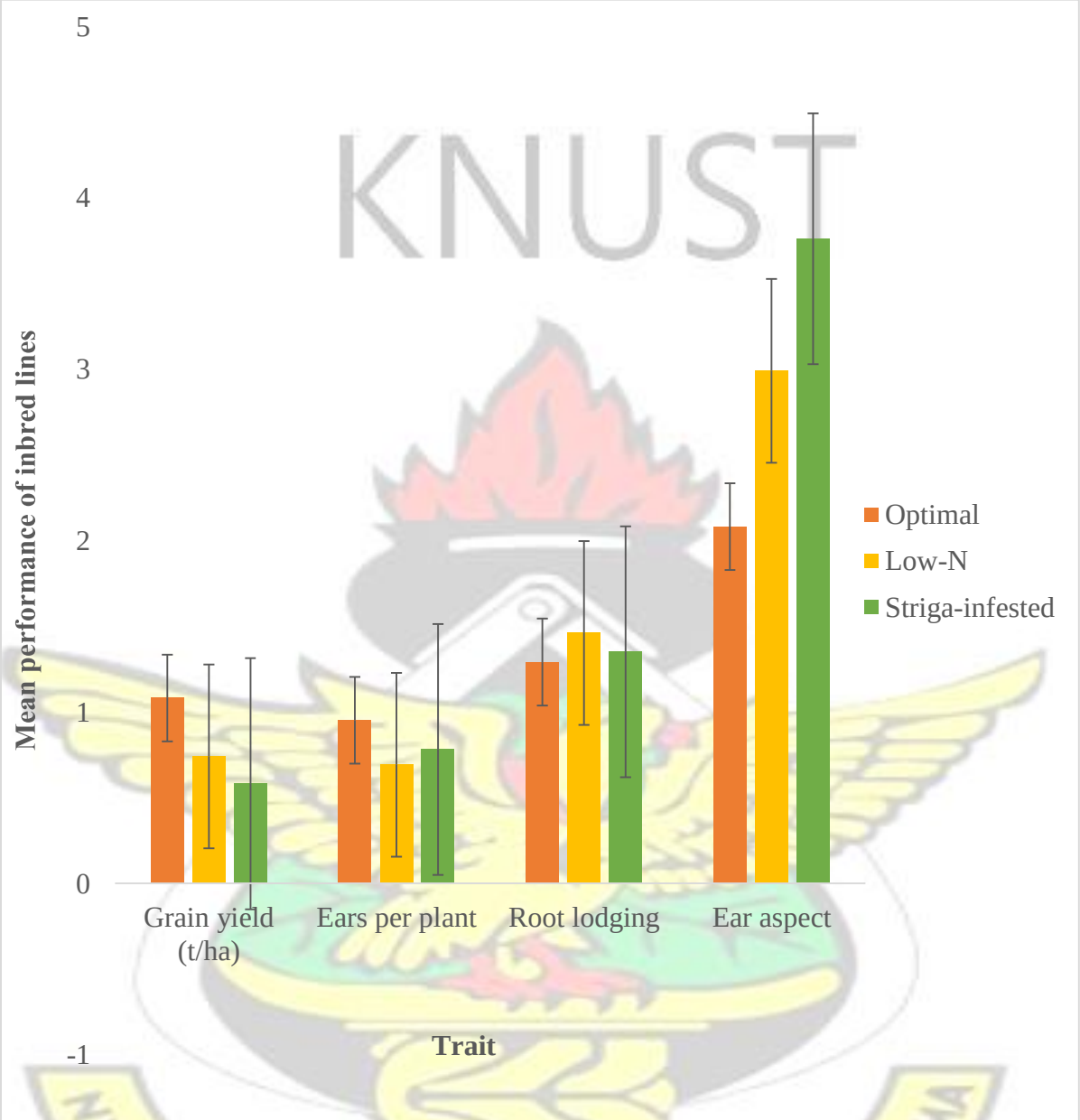

Figure 4. 2 Mean grain yield (t/ha), ears per plant, root lodging and ear aspect of the 100 inbred lines evaluated across optimal growing conditions, *Striga*-infested and lowN environments

4.3.3 Path coefficient analysis of grain yield and other traits

The results of the regression analysis revealed that the independent traits studied accounted for 47%, 36% and 44% of the total variation in grain yield (dependent trait) under optimal, *Striga*-infested and low-N conditions, respectively (Tables 4.6, 4.7 and 4.8). Under optimal growing conditions, plants per plot (0.48), ear aspect (0.25) and ears per plot (0.5) had the highest correlation with grain yield. Days to silking (0.78), ears per plot (0.69), days to anthesis (-0.49) and anthesis-silking interval (-0.36) were traits with high direct effects on grain yield (Table 4.6). Days to silking had an indirect effect on grain yield through days to anthesis (-0.41) and ASI (-0.19), while days to anthesis had an indirect effect on grain yield through days to silking (0.65). Ears per plot indirectly contributed to grain yield through ears per plant (-0.16) (Table 4.6).

Ear aspect (-0.51), plants per plot (0.37) and ears per plot (0.45) had the highest association with grain yield under artificial *Striga* infestation (Table 4.7). The highest negative direct effect on grain yield was obtained by ear aspect (-0.66). Also, plant height (-0.34), days to silking (-0.31) and STRRAT2 (-0.23) had low negative direct effects on grain yield. Ears per plot ().32) had a positive indirect effect on grain yield. Plants per plot had indirect contribution to grain yield through ears per plot (0.27) and STRRAT2 (-0.06). Plant height (0.28), ears per plot (-0.03) and days to silking (0.04) had indirect effects on grain yield through ear aspect. Ear height indirectly contributed to grain yield through plant height (0.04) while days to anthesis had an indirect effect on grain yield through days to silking (0.18) (Table 4.7).

Under low-N environments, traits such as days to anthesis (-0.75), days to silking (-0.68) and ears per plant (0.64) had high associations with grain yield (Table 4.8). Days to silking (0.31) and ears per plant (0.44) had the highest positive direct effects on grain yield, while days to anthesis (-0.93) had the highest negative direct effect on grain yield. Stay green characteristic (-0.20) and ear aspect (-0.05) had a lower negative indirect effect on grain yield, while plant aspect (0.00) had no effect on grain yield. Days to anthesis contributed indirectly to grain yield through ears per plant (-0.08) and days to silking (0.29) (Table 4.8).

Table 4.

6 Path analysis of the effects of various traits on grain yield of the inbred lines under optimal growing conditions

Trait	Correlation Coefficient	Direct Effect	Indirect Effects											
			PH	EH	ASI	SL	RL	PHARV	PASP	EHARV	EASP	EPP	DYSK	DA
PH	0.04	0.18		0.14	-0.06	-0.03	0.01	0.01	0.00	0.02	-0.03	0.02	-0.03	0.00
EH	0.03	-0.26	-0.20		0.10	0.01	0.00	-0.05	-0.03	-0.05	0.05	-0.02	0.02	-0.04
ASI	0.09	-0.36	0.11	0.14		0.00	0.01	0.04	0.02	0.04	0.04	0.03	-0.19	0.01
SL	0.04	-0.08	0.01	0.00	0.00		-0.01	-0.02	-0.01	-0.01	0.00	0.01	0.01	0.01
RL	-0.01	-0.03	0.00	0.00	0.00	-0.01		0.00	0.00	0.00	0.00	0.00	0.01	0.01
PHARV	0.48	0.04	0.00	0.01	0.00	0.01	0.00		0.01	0.03	-0.01	0.00	0.00	0.00
PASP	0.12	0.02	0.00	0.00	0.00	0.00	0.00	0.00		0.00	-0.01	0.00	0.00	0.00
EHARV	0.50	0.65	0.08	0.13	-0.07	0.08	0.04	0.47	0.13		-0.16	0.37	-0.05	-0.01
EASP	-0.25	-0.14	0.02	0.03	0.01	0.01	0.00	0.02	0.04	0.03		0.02	0.01	0.00
EPP	0.11	-0.29	-0.03	-0.03	0.02	0.05	0.01	0.01	-0.04	-0.16	0.04		0.00	-0.01
DYSK	0.16	0.78	-0.12	-0.07	0.42	-0.07	-0.14	-0.03	-0.03	-0.06	-0.04	-0.01		0.65
DA	0.13	-0.49	-0.01	-0.08	0.01	0.05	0.09	-0.01	0.01	0.01	0.00	-0.01	-0.41	
Regression Statistics														
R^2		0.47												
Standard Error		0.84												
Observations (n)		100												

Table 4.

PH, plant height; EH, ear height; ASI, anthesis-silking interval; SL, stalk lodging, RL, root lodging; PHARV, plants per plot; EHARV, ears per plot; EASP, ear aspect; EPP, ears per plant, DYSK, days to silking, DA, days to anthesis.

7 Path analysis of effects of various traits on grain yield of the inbred lines under artificial *Striga* infestation

Trait	**Correlation coefficient**	**Direct effect**	**Indirect effect**							
			EASP	EH	PH	PHARV	EHARV	STRRAT2	DYSK	DA
EASP	-0.51	-0.66		0.07	0.28	0.02	0.05	0.03	0.04	0.05
EH	-0.22	-0.20	0.02		-0.04	0.01	0.01	0.02	-0.01	0.00
PH	-0.06	-0.34	0.15	-0.07		-0.03	-0.01	0.03	-0.02	-0.02
PHARV	0.37	0.15	0.00	0.00	0.01		0.12	0.04	-0.01	-0.01
EHARV	0.45	0.32	-0.03	-0.01	0.01	0.27		0.08	-0.03	-0.03
STRRAT2	-0.04	-0.23	0.01	0.02	0.02	-0.06	-0.05		0.01	0.00
DYSK	-0.15	-0.31	0.02	-0.01	-0.01	0.03	0.03	0.01		-0.26
DA	-0.04	0.21	-0.02	0.00	0.01	-0.01	-0.02	0.00	0.18	
Regression Statistics										
R^2		0.36								
Standard Error		0.95								
Observations (N)		100								

Table 4.

EASP, ear aspect; PH, plant height; EH, ear height; PHARV, plants per plot; EHARV, ears per plot; STRRAT2, *Striga* damage syndrome rating, DYSK, days to silking, DA, days to anthesis

8 Path analysis of the effects of various traits on grain yield of the inbred lines under low soil nitrogen environment

Trait	Correlation coefficient	Direct effect	Indirect effect								
			EPP	DYSK	DA	PASP	EASP	LD	PH	EH	RL
EPP	0.64	0.44		-0.10	-0.08	-0.09	-0.04	-0.12	0.00	0.07	-0.02
DYSK	-0.68	0.31	-0.07		0.29	0.05	0.01	0.03	0.03	-0.05	0.02
DA	-0.75	-0.93	0.17	-0.87		-0.16	-0.04	-0.09	-0.09	0.17	-0.05
PASP	-0.32	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
EASP	-0.13	-0.05	0.00	0.00	0.00	-0.01		0.00	0.00	0.00	0.00
LD	-0.42	-0.20	0.06	-0.02	-0.02	-0.06	-0.01		0.01	0.01	0.02
PH	0.16	0.13	0.00	0.01	0.01	-0.01	0.01	0.00		0.04	0.00
EH	0.45	0.21	0.03	-0.03	-0.04	-0.03	-0.01	-0.01	0.07		0.00
RL	-0.05	-0.02	0.02	0.02	0.02	-0.01	-0.01	-0.02	0.00	0.00	
Regression Statistics											

Table 4.

R^2	0.44
Standard Error	0.78
Observations (n)	100

EPP, ears per plant, DYSK, days to silking, DA, days to anthesis; EASP, ear aspect; LD, stay green characteristic; PH, plant height; EH, ear height; RL, root lodging

4.3.4 Genotype by Trait (GT) and Trait Association by Environment (ABE) analyses

The biplots presented in Figures 4.3, 4.4 and 4.5 showed that 55.9%, 58.5% and 51.0% of the total variation of the environment-centered G x E of the multi-trait data of the inbred lines under optimal, low-N and *Striga*-infested environments, respectivel, and were therefore appropriate for visualizing the associations among traits in the respective environments. The lines that connect the traits to the biplot origin are called Tester (trait) vectors. The correlation between the traits is approximated by cosine of the angle between their vectors (Kroonenberg, 1995). The biplot in Figure 4.3 presented the trait association among grain yield and other traits under optimal growing conditions. The biplot showed a close acute angle between DS and DA; between EPP and GYLD, and between PHARV and EHARV, indicating a strong positive correlation between each pair of traits under optimal growing conditions. The angle between the following traits were also acute: GYLD and PH; GYLD and EHARV, GYLD and PHARV, PHT and DS; and PHT and DS, showing that these traits were positively correlated. On the contrary, the angles between EASP and EPP and EASP and GYLD were obtuse, indicating negative correlation between them. The inbred line TZdEI 233 was the vertex inbred line where PHT, DA and DS fell. The inbred line TZEI 472 was the vertex inbred line where EPP, EHARV and PHARV fell. The inbred lines TZdEI 283 and TZEI 471were the vertex inbred lines for GYLD and EASP, respectively (Figure 4.3).

The biplot in Figure 4.4 showed a close acute angle between DS and DA, PHARV and EHARV and GYLD and PHT under low-N environments. This indicated a close positive correlation between each pair of traits. The angle between GYLD and DS and DA as well

as between GYLD and PHARV and EHARV were acute but wide, indicating a weak positive correlation among those traits. There was an obtuse angle between EASP and GYLD, PHT, PHARV and EHARV, but the obtuse angle between EASP and GYLD and PHT was the widest. This indicated very strong negative correlation between EASP and GYLD and PHT. The inbred line TZEI 471 was the vertex inbred line where EASP fell. TZdEI 213 was the vertex inbred line where DA and DS fell, while TZEI 124 was the vertex inbred line where GYLD, PHT, EHARV and PHARV fell (Figure 4.4).

Under *Striga*-infested environments, GYLD had an acute angle with EHARV and PHARV but an obtuse angle with PH and DS (Figure 4.5). This showed positive association between GYLD and EHARV and PHARV, and negative association between GYLD and PH and DS. The EASP had a close acute angle with STRRAT2 but had an obtuse angle with GYLD, EHARV and PHARV. This showed that EASP and STRRAT2 was closely correlated, while EASP had a negative correlation with GYLD, EHARV and PHARV. The vertex inbred line for EHARV, PHARV and GYLD was TZdEI 120, where TZEI 124 was the vertex inbred line for PH and DS. The inbred lines TZEI 471 and TZEI 41 were vertex inbred line for STRRAT2 and EASP, respectively (Figure 4.5). The Association by Environment (ABE) biplot in Figure 4.6 explained 99.5% of the variation of the total sum of squares in the multi-trait data on the inbred lines across optimal, low-N and *Striga*infested environments. The biplot revealed that DS, DA, EHARV and PHARV are explanatory traits with the highest influence on GYLD across all the test environments, except for low-N in 2014. The following nine inbred lines were the most superior across all research conditions: TZEI 56, TZdEI 283, TZEI 18, TZEI 31, TZEI 35, TZEI 379, TZEI 476, TZEI 124, and TZEI 13.

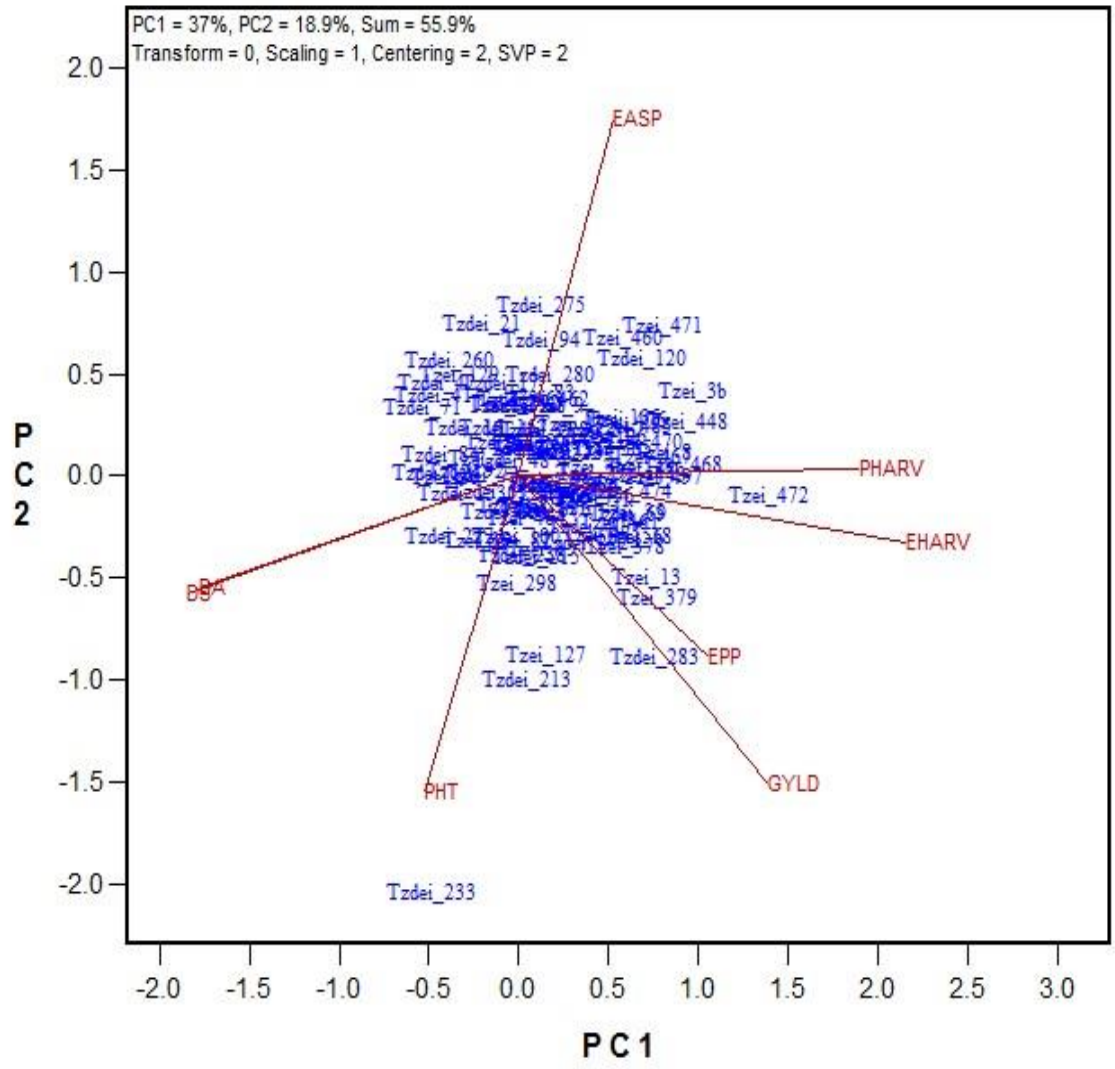
PC1 = 37%, PC2 = 18.9%, Sum = 55.9%
Transform = 0, Scaling = 1, Centering = 2, SVP = 2
EASP
PHARV
EHARV
Tzei_472
Tzei_3b
Tzei_448
Tzei_471
Tzei_460
Tzei_120
Tzei_275
Tzei_21
Tzei_94
Tzei_260
Tzei_280
Tzei_298
Tzei_13
Tzei_379
Tzei_127
Tzei_213
Tzei_283
EPP
PHT
GYLD
Tzei_233
PC 2
PC 1

Figure 4. 3 Genotype by trait biplot based on multi-trait data of the 100 inbred lines evaluated at Kwadaso and Nyankpala in 2015 under optimal growing conditions. † DS, days to silking; DA, days to anthesis; PHT, plant height; GYLD, grain yield; EPP, ears per plant; EHARV, ears per plot; PHARV, plants per plot; EASP, ear aspect

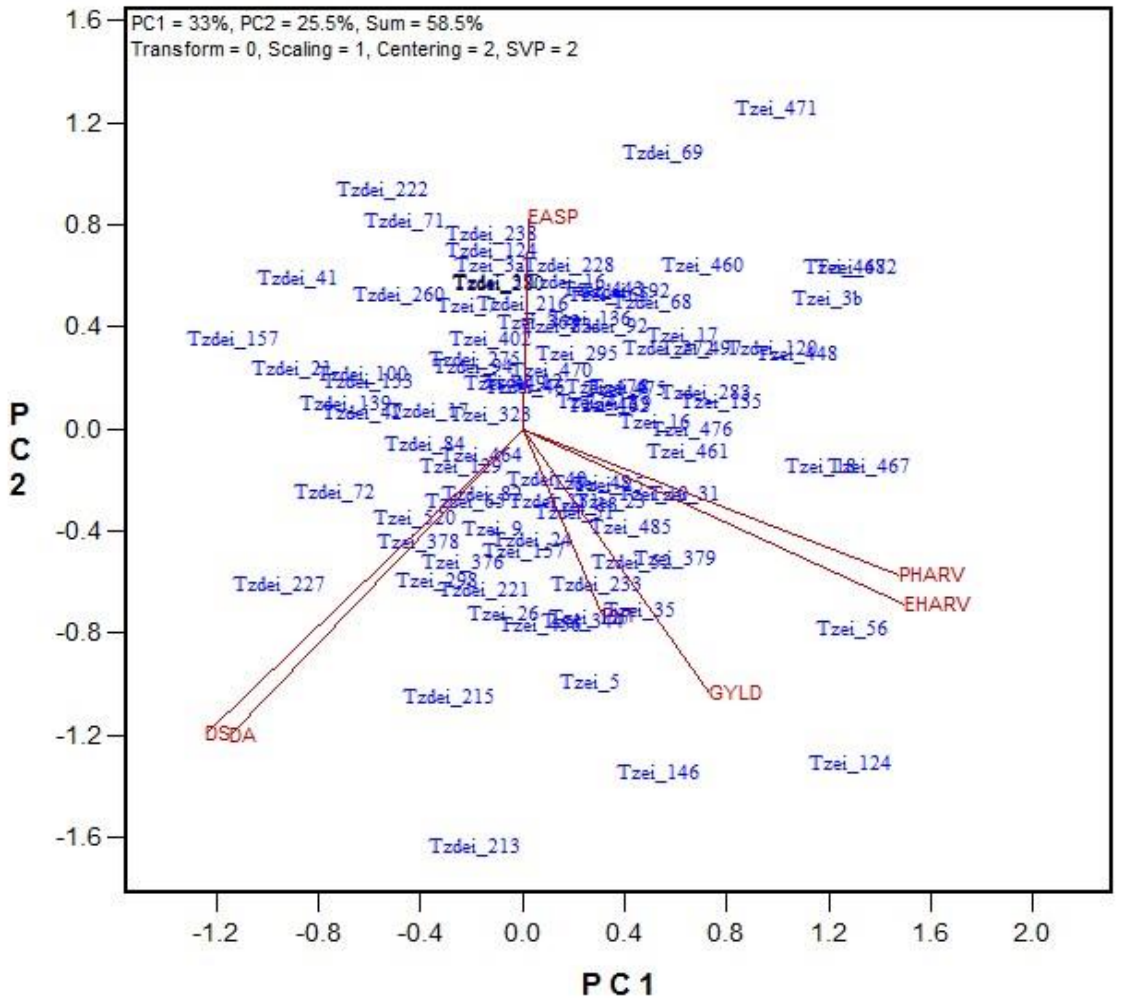

Figure 4. 4 Genotype by trait biplot based on multi-trait data of the 100 inbred lines evaluated at Kwadaso in 2014 and 2015 under low-N environments. † DS, days to silking; DA, days to anthesis; PHT, plant height; GYLD, grain yield; EHARV, ears per plot; PHARV, plants per plot; EASP, ear aspect

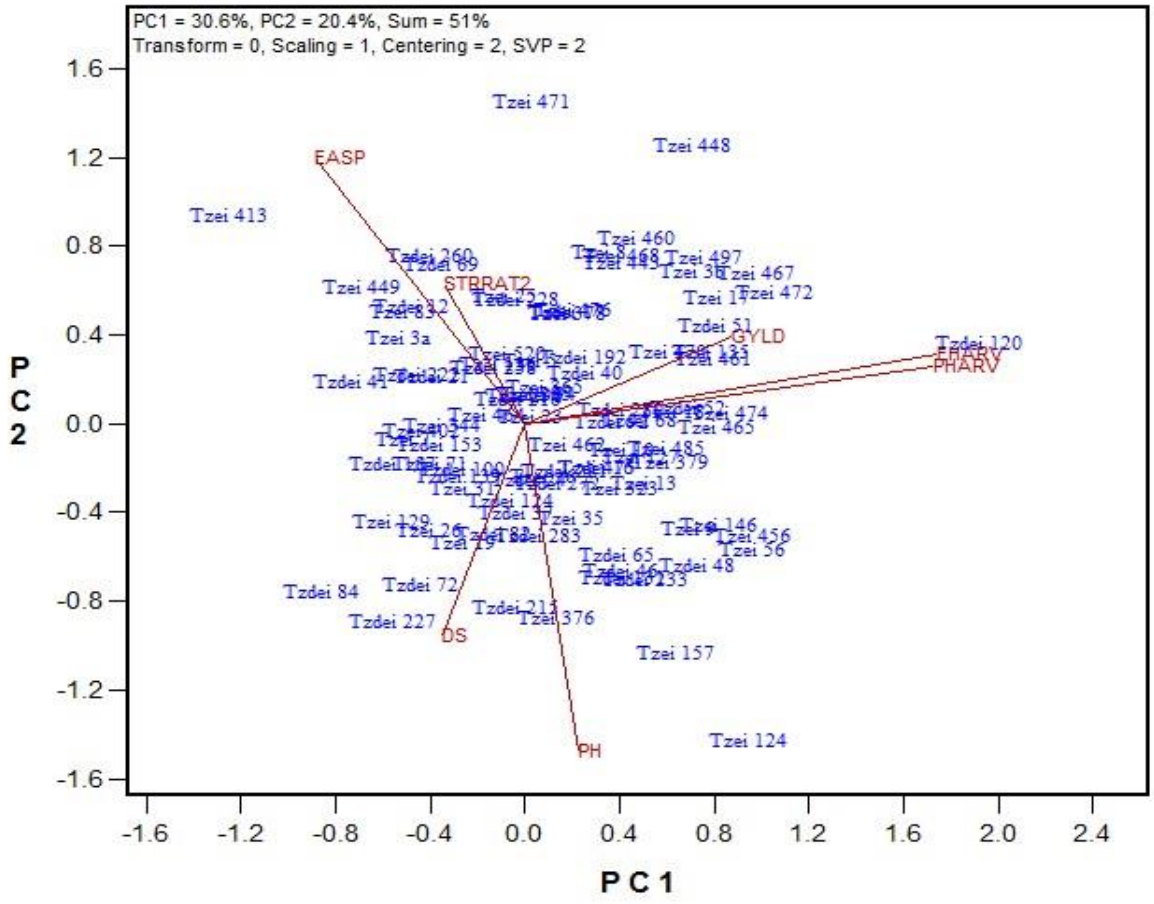

Figure 4. 5 Genotype-by-trait biplot based on multi-trait data of 100 inbred lines evaluated at Nyankpala in 2014 and 2015 under artificial *Striga* infestation. † DS, days to silking; PH, plant height; GYLD, grain yield; EHARV, ears per plot; PHARV, plants per plot; EASP, ear aspect; STRRAT2

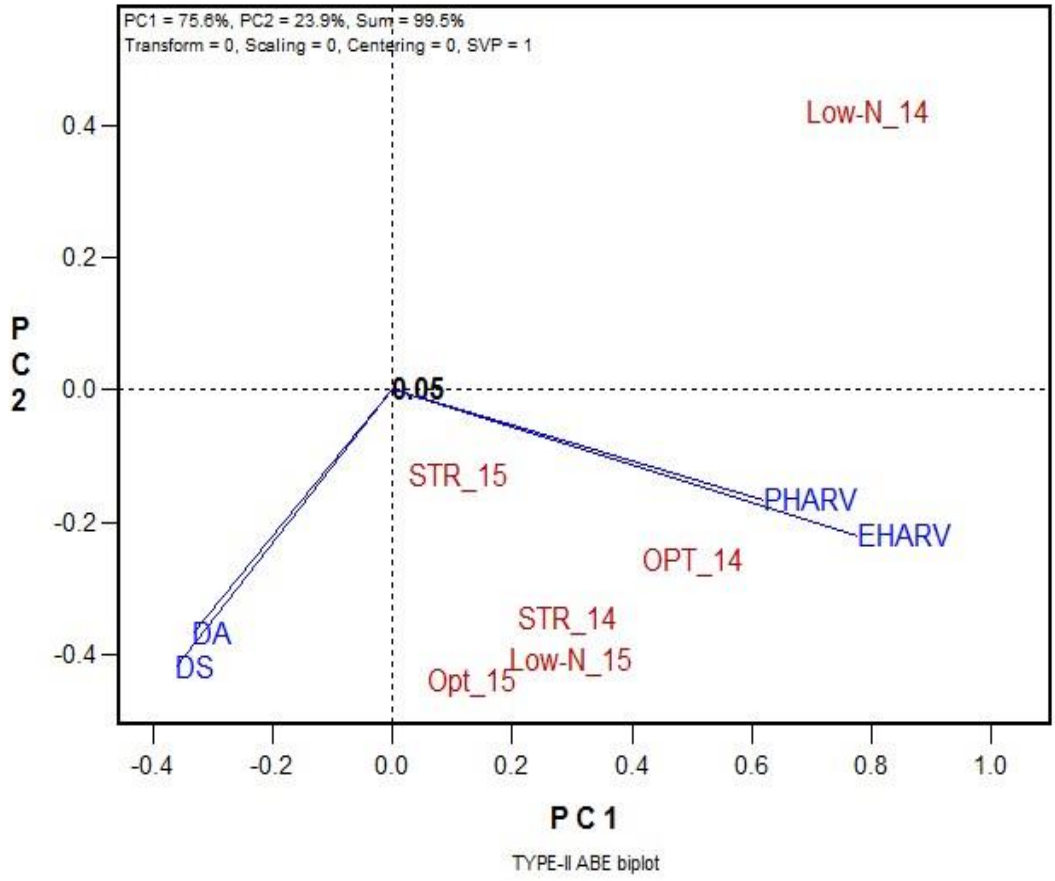

Figure 4. 6 Trait association by environment biplot showing the correlations of days to anthesis, days to silking, plants and ears per plot with grain yield across the six test

environments in 2014 and 2015. † DS, days to silking; DA, days to anthesis; EHARV, ears per plot; PHARV, plants per plot

4.4 Discussion

The observed significant genotypic, environment and GEI mean squares for most measured traits under *Striga* infestation, low-N and optimal growing environments indicated that the test environments were unique and diverse, and provided important information on the inbred lines. It also indicated that there is adequate genetic variability among the inbred lines to allow significant progress to be made from selection for *Striga* resistance and lowN tolerance. The existence of genetic variability among the inbred lines also indicated that they could serve as parents for the development of productive hybrids for optimal, *Striga* endemic and low-N environments. Similar findings were reported by Badu-Apraku *et al*. (2012; 2013) and Akaogu *et al*. (2012). Across the six test environments, the inbred lines exhibited wide phenotypic variation among measured traits. However, the significant genotypic and environmental mean squares for grain yield, days to anthesis and silking, plant height, ear height, ear aspect and ears per plot across *Striga*-infested, low-N and optimal growing environments revealed the importance of these traits in the selection of inbred lines with superior performance across these research conditions. This result corroborated the findings of Menkir and Akintunde, (2001) and Badu-Apraku *et al*., (2004b; 2011a; 2012). The significant interaction between genotype and environment for

grain yield, days to anthesis and silking, plant height, ear aspect and ears per plant across the six test environments indicated that the expression of these traits will not be consistent in varying environments and years. These results confirmed the need to specifically evaluate the inbred lines under the different environments and years in order to identify *Striga* tolerant/resistant and/or low-N tolerant inbred lines with consistently favorable response to either one or both stresses (Meseka *et al.,* 2006; Makumbi *et al.* 2011; Menkir *et al*., 2003; 2013; Badu-Apraku *et al*., 2012; 2013).

Grain yield of the inbred lines was reduced by 22% under low-N compared to yield under optimal growing conditions. The observed delay in silking together with wider anthesissilking interval under low-N might have induced barrenness thus contributing to yield reduction under low-N. Maize ear has a relatively weak sink capacity at flowering. Therefore, during flowering a reduction in nitrogen availability can reduce the flux of assimilates to the ear resulting in delay of silking, and an increase in anthesis-silking interval. Reduction in assimilates can also lead to kernel abortion, barren plants, and ultimately reduced grain yield (Edmeades *et al*., 1993; Elings *et al.*, 1997). The marked reduction in plant height and increase in root lodging under low-N reflected the general reduction in plant growth rate that may have contributed to yield reduction under low-N. Chun *et al.* (2005) observed that maize plants responded to N deficiency by enhancing lateral root growth with a reduction in the number of axial roots. Ultimately, the total amount of roots is usually less for plants grown under N stress than those under normal N which usually increases root lodging under low-N. Remobilization of nitrogen reserves from the leaves to the grain during the post-silking growth phase in maize leads to leaf senescence particularly in a nitrogen deficient environment (Rajcan and Tollenaar, 1999a;

1999b). This may result in a decline in the radiation use efficiency, photosynthesis and restrict the attainment of potential yield (Muchow and Sinclair, 1994). Maize genotypes with stay green characteristic have greater tolerance to post-silking environmental stresses (Tollenaar *et al*., 1994), which include reduction in N uptake and prolonged leaf longevity (Hay and Porter, 2006) which sustain photosynthetic activity at a time of decline but high crop demand (Kosgey *et al*., 2010). These attributes make stay green characteristic an important component of genetic variation in nitrogen-use efficiency in maize (Bänziger *et al*., 2000). In the present study, stay green characteristic did not seem to have a significant effect on grain yield in any specific pattern. Similar results were observed by Chapman & Edmeades (1999), Monneveux *et al.* (2006; 2008) and Badu-Apraku and Fakorede (2017) under drought stress. Overall, the results suggested that days to silking, ears per plant, plant height and root lodging may be more reliable measures of low-N tolerance of the inbred lines than stay green characteristic. The following seventeen lines were identified as lowN tolerant and could serve as parents of low-N tolerant hybrids and synthetics: TZEI 449,

TZEI 365, TZEI 485, TZEI 468, TZdEI 238, TZEI 471, TZdEI 283, TZdEI 272, TZEI 3B, TZEI 472, TZEI 18, TZEI 470, TZdEI 100, TZEI 378, TZEI 13, TZEI 344 and TZEI 475.

Striga infestation significantly reduced grain yield and almost all yield components studied. On average, the inbred lines suffered 36% yield reduction under *Striga* infestation compared to the yield performance under optimal conditions. The inbred lines suffered severe reduction in ear aspect (26%) and ears per plant (21%). This result suggested that ear aspect, and ears per plant are the key traits to consider when selecting early maturing *Striga* resistant inbred lines for improved yield under *Striga*-infested conditions. These

results are consistent with the findings of similar studies involving early maturing inbred lines and hybrids by Adetimirin *et al.* (2000) and Badu-Apraku *et al*. (2010). Adetimirin *et al,* (2000) reported that pre-flowering stress due to *Striga* parasitism is higher than postflowering stress and results in higher reduction of ears per plant (44%) than reductions for other yield components (12±29%). The performance of the inbred lines in respect of key *Striga* adaptive traits such as *Striga* damage syndrome rating and number of emerged *Striga* plants was outstanding. Generally, the inbred lines supported considerably fewer numbers of emerged *Striga* plants of 9 and 21 plants per plot, respectively at 8 and 10 WAP. The number of emerged *Striga* plants recorded in this study is below the range of 21-31 *Striga* plants at 8 WAP, and 24-39 emerged *Striga* plants at 10 WAP reported by previous workers (Badu-Apraku and Oyekunle, 2012 and Badu-Apraku *et al*., 2010; 2013 and Akinwale *et al*., 2013). The fewer number of emerged *Striga* plants recorded in this study may have been influenced by the large number of test inbred lines with *Zea diploperennis* genetic background. According to Lane *et al*. (1997), genotypes with genes from *Zea diploperennis* restrict the penetration of its roots by *Striga* plants and impair the development and survival of *Striga* parasites. Amusan *et al.* (2008) observed morphological differences between roots of susceptible maize inbred lines and resistant inbred lines derived from *Zea diploperennis*. The authors found that the resistant inbred line had fewer *Striga* attachments, delayed parasitic development and higher mortality of attached parasites compared with the susceptible inbred line, suggesting that the resistant inbred line produced a developmental barrier and incompatible response against *Striga* parasitism. Relating the current results to the findings of Lane *et al,* (1997) and Amusan *et al.* (2008), it may be concluded that the fewer numbers of emerged *Striga* plants recorded in this study

indicates the presence of inbred lines with desirable alleles for resistance to *Striga* which could be used to develop more stable *Striga* resistant hybrids and synthetics. The *Striga* resistant inbred lines could also serve as sources of *Striga* resistant alleles for population improvement. The selection index used to select superior inbred lines under *Striga*-infested environment revealed that

49% of the inbred lines may possess some level of tolerance and/or resistance to *Striga*. Out of the 49 inbred lines with positive base index, the lines TZEI 485, TZEI 146, TZEI 16, TZEI 456, TZEI 127, TZEI 13, TZEI 461, TZEI 365, TZEI 136, TZEI 25, TZEI 472, TZdEI 216, TZdEI 215, TZEI 468 and TZEI 157 were characterized as *Striga* tolerant because they had high grain yield and lower *Striga* damage syndrome ratings.

Striga parasitism is known to intensify with increased deterioration of soil fertility (Menkir *et al.*, 2001), implying that varieties targeted to *Striga* endemic areas must not be only *Striga* resistant/tolerant but also be adapted to low-N environments and should be able to utilize applied N more efficiently. Thus, the inbred lines TZEI 127, TZdEI 283, and TZEI 146. TZEI 485, TZEI 344, TZEI 35, TZEI 124, TZEI 376, TZEI 13, TZdEI 272, TZdEI 215, TZdEI 216, TZEI 379, TZEI 10, TZEI 365, TZEI 25 TZEI 56, TZdEI 69, TZEI 136 and TZEI 157, identified by the multi-trait selection index to be superior across optimal growing conditions, *Striga*-infested and low-N environments would be very useful in breeding multiple-stress tolerant (*Striga* and low-N) hybrids.

Grain yield is a quantitative trait, and is functionally related to yield components particularly when evaluated under stress. Breeder's knowledge of the degree of association among grain yield and its component traits is crucial, given that the selection of certain traits changes the behavior of other traits in crops (Akintunde, 2012). The results of the

path analyses revealed that days to silking, ears per plot, days to anthesis and anthesissilking interval have the highest direct effect on grain yield under optimal conditions, while ear aspect, plant height, days to silking, STRRAT2 and ears per plot were traits with the highest direct influence on yield under *Striga* infestation. Under low-N, days to silking, ears per plant and days to anthesis were the most important traits with direct effect on grain yield. The results indicated that these traits could be used for indirect selection of improved grain yield under optimal, *Striga* and low-N environments. Badu-Apraku (2007), Menkir and Akintunde (2001) and Badu-Apraku *et al.* (2004b, 2011a, 2012) reported similar trait associations under similar environments. The path analysis also revealed that the direct and indirect effects of some of the measured traits on grain yield were very small, while others were inconsistent in direction across environments. The direct effect of days to anthesis on grain yield was moderately weak (0.49) under optimal conditions, but approached 0.93 under low-N. Also, the direct effect of ears per plant on grain yield increased from -0.29 to 0.44 under optimal and low-N environments, respectively. Moreover, the indirect effect of days to silking on grain yield through days to anthesis and ears per plant also increased under low-N. These results are consistent with reports by Edmeades *et al.* (1997) and Bänziger *et al*. (2000) who reported that correlation between grain yield and other yield components becomes stronger under stress. These results also showed a strong dependence of grain yield on flowering traits and hence corroborated the findings by Edmeades *et al.* (1997), Bänziger *et al*. (2000), Badu-Apraku *et al*. (2012) on the effects of nitrogen deficiency on flowering, pollination and ear-setting processes of maize, and their consequent effects on yield of a genotype under nitrogen deficient environment. The positive phenotypic correlation of days to anthesis and days to

silking with grain yield under optimal growing conditions; the positive indirect effect of days to anthesis on yield through days to silking under optimal and low-N environments, as well as the positive direct effect of days to anthesis on grain yield under *Striga* infestation, suggested that generally the late maturing inbred lines performed better than those that matured early under optimal growing conditions, *Striga*-infested and low-N environments. Sharifi and Namvar (2016) also found that yield potential of maize increased with increased days to anthesis and silking. Similarly, Badu-Apraku and Fakorede (2017) observed that selection for improved yield under artificial *Striga*-infested and *Striga*-free environments in the source population, TZEE-W Pop STR resulted in increased days to anthesis and silking under low-N (30-50 kg N ha^{-1}), and increased days to silking under high-N (120 kg N ha^{-1}). They also observed that selection in the source population, TZEE-Y Pop STR induced increased days to anthesis, ear height, and decreased anthesis–silking interval

(Badu-Apraku and Fakorede, 2017).

Plant and ear heights usually have a positive association with grain yield in maize, therefore, the observed negative direct and indirect effects of plant and ear heights on grain yield under *Striga* infestation is noteworthy. This result suggested that a reduction in plant and ear heights could improve the relative grain yield of maize inbred lines in *Striga*infested environments, implying that shorter plants are more adapted to *Striga* infestation than taller ones. Theoretically, shorter plants have lower amount of vegetative biomass which reduces resource use per plant for vegetative growth and maintenance, resulting in greater resource availability for grain production (Sangoi and Salvador, 1998). Although, no report in literature was found of an experiment with the specific purpose of

evaluating the possible advantages of short stalked maize cultivars over tall ones in *Striga*-infested environments. There is some indirect evidence derived from experiments that indicate reduction in plant height has the potential for improving tolerance to stress in general and specifically to drought tolerance in maize. Kasele *et al*. (1994) observed in experiments with growth retardants that a reduction in plant height has the potential for improving resistance to drought in maize. Bolaños *et al*. (1993) observed that selection for improved performance under drought in Tuxpeno Sequia resulted in a slight reduction in plant height.

The trait assciations revealed by the Genotype-by-Trait biplots are consistent with the main patterns of trait associations revealed by the path coefficient analyses under optimal conditions, low-N and *Striga*-infested environments. The results of the Genotype-by-Trait biplots showed that high yielding inbred lines in optimal growing conditions tended to be taller, have high number of ears per plant and have high number of ears per plot and plants per plot. On the other hand, inbred lines with low grain yield had contrasting trait profile. In an earlier study involving extra-early maturing hybrids by Adu *et al. (*2016), higher grain yield was associated with increased plant height, number of plants and ears per plot as well as good ear aspect under optimal conditions. The best inbred line for grain yield was TZdEI 283. The inbred line TZEI 472 was the best inbred in terms of ears per plant, as well as ears and plants per plot. The inbred line TZEI 471 had the poorest ear aspect, while TZdEI 233 had the highest plant height, days to anthesis and silking.

Under low-N environments, high yielding inbred lines had taller plants, high numbers of plant and ears per plot; they were late maturing and had good ear aspect. This result

indicated that plant height, ear aspect, days to silking and number of plants and ears per plot are valuable traits in the selection of high grain yields under low-N environments. This result is consistent with the findings of Badu-Apraku *et al*. (2010). Using Genotype-byTrait biplot analyses, Badu-Apraku *et al*. (2010) found plant height and ear aspect as dependable traits for indirect selection of high yielding genotypes in nitrogen deficient and moisture-stressed environment. The observed strong negative correlation between ear aspect and plant height indicated that inbred lines with taller plants will have good ear aspect (ear aspect is measured such that high value means less desirable). Also, the strong positive correlation between yield and plant height indicated that taller plants will have high grain yield in nitrogen deficient environments. However, the association between plant height and both ear aspect and grain yield may be undesirable, since increased plant height increases lodging with negative consequences on ear aspect and grain yield. Therefore, the use of plant height as an indirect selection criterion for improved yield should be done cautiously. Under low-N, the inbred line with the poorest ear aspect was TZEI 471. The inbred line TZdEI 213 had the longest days to anthesis and silking, while TZEI 124 had the highest grain yield, plant height and number of ears and plants per plot.

The pattern of associations among the traits identified under artificial *Striga* infestation indicated that high yielding inbred lines in *Striga*-infested environments had larger numbers of ear and plant per plot, shorter plants and were early maturing. Poor yielding inbred lines had contrasting characters to those of the high yielding ones. Although, *Striga* damage syndrome rating at 10 WAP (STRRAT2) and ear aspect had the weakest negative correlation with grain yield, their association with ears and plant per plot makes them traits

with the highest indirect effects on grain yield. The strongest association observed between *Striga* damage syndrome rating at 10 WAP and ear aspect indicated that ear aspect could be used in place of *Striga* damage syndrome rating at 10 WAP in selection programs without sacrificing information on the inbred lines. Both ear aspect and *Striga* damage syndrome rating at 10 WAP are subjective, and require experience in measurement to minimize the effects of the subjectivity (Badu-Apraku and Fakorede, 2017). However, judging the suitability of both traits on how timely the information will be available to aid other decisions, *Striga* damage syndrome rating at 10 WAP becomes the most ideal secondary trait for preliminary selection since it can be measured before maturity (10 WAP) as compared to ear aspect which is measured during final harvesting. The inbreds lines TZdEI 120 was the best for ears per plot, plants per plot and grain yield while TZEI 124 had the highest plant height and days to silking. The inbred lines TZEI 471 and TZEI 413 had the poorest *Striga* damage syndrome rating at 10 WAP and ear aspect, respectively. The ABE biplot analysis identified days to anthesis, days to silking, plants and ears harvested per plot as the most important traits with the highest influence on grain yield of the inbred lines across optimal, low-N and *Striga*-infested environments. Using these four traits and grain yield in a multi-trait selection index, TZEI 56, TZdEI 283, TZEI 18, TZEI 31, TZEI 35, TZEI 379, TZEI 476, TZEI 124, and TZEI 13 were identified as the most adapted inbred lines across the test environments. They may therefore be suitable parents for hybrids with improved grain yield across the three research conditions. Generally, all the promising inbred lines identified for each of the test environments may be the optimal choice of parental lines for developing hybrids with maximum expression of tolerance to low-N and *Striga* infestation. However, since the per se performance of

inbred lines is not a good indicator of the performance of the resulting hybrids, especially for grain yield (Mohammadi *et al*. 2008), there was the need to evaluate the inbred lines in hybrid combinations under the target environments to identify those with high combining abilities and better hybrid responses in the target environments

CHAPTER FIVE

5.0 Genetic analysis of early maturing maize inbred lines under optimal growing conditions, *Striga*-infested and low soil nitrogen environments

5.1 Introduction

Information on the nature, mode of inheritance and combining ability of inbred lines is crucial in determining the breeding value of an inbred line, identifying superior parents for hybrid development and the appropriate selection procedures to use in a breeding program (Badu-Apraku *et al.*, 2013; 2017). Combining ability analysis has been used extensively to elucidate the mode of inheritance of *Striga* resistance in maize (Kim, 1994, 1991) and the mode of inheritance of tolerance to low soil nitrogen in maize (Kling *et al.*, 1997, Betran *et al*., 2003b; Meseka *et al*., 2006). Combining ability studies are also employed in heterotic groupings of maize lines. Three combining ability derived methods used in heterotic groupings are specific combining ability (SCA) effect of grain yield (Fan *et al.*, 2004), heterotic group's specific and general combining ability (HSGCA) (Fan *et al*., 2008) and general combining ability effects of multiple traits (HGCAMT) (Badu-Apraku *et al.*, 2013b). However, the efficiencies of these methods are influenced by the kind of germplasm used (Badu-Apraku *et al.*, 2016).

More recently, molecular marker based genetic distances (GD) are also employed in heterotic grouping studies (Lanza *et al*., 1997; Balestre *et al*., 2008). However, heterotic grouping based on molecular markers has also produced contradictory results depending

on the type of germplasm used, the type of markers used (Hamblin *et al*., 2007) and the type of platform used for genotyping a given marker type (Semagn *et al*., 2012, 2014).

Reports by Suwarno *et al.* (2014) revealed that SNP-based GD was slightly better than SCA based heterotic grouping in maize. Among HSGCA, SCA and SSR based genetic distance grouping methods, Akinwale *et al*. (2014) identified HSGCA as the most effective method in classifying 28 early maturing inbred lines under both *Striga*-infested and *Striga*free environments. Badu-Apraku *et al*. (2015) identified the SNP-based GD method as the most efficient method among HGCAMT, HSGCA, and SCA effect of grain yield in grouping 14 early maturing QPM inbred lines under *Striga*-infested, drought, low-N and optimal environments. In Badu-Apraku *et al*. (2015), the HSGCA method was the most efficient in grouping 17 IITA and CIMMYT maize inbred lines under drought, low-N and optimal environments followed by the HGCAMT, SNP-GD method and the SCA effect of grain yield methods.

There is scanty information on the comparative efficiency of the HGCAMT, SSR and SNP marker-based GD methods in heterotic groupings of IITA maize inbred lines. A good understanding of the relative efficiencies of these methods in assigning breeding lines into heterotic groups will not only enhance the selection gains of breeders, but will also reduce the cost of variety evaluation associated with the use of all three methods at a time. Furthermore, information on mode of inheritance of *Striga* resistance and low-N tolerance of newly developed inbred lines of IITA would facilitate the development and deployment of multiple-stress tolerant hybrids to farmers and seed producers in West and Central African countries. The objectives of the present study were to:

i. Determine the combining ability for grain yield and agronomic traits of selected set of early maturing inbred lines under *Striga* infestation, low-N and optimal growing conditions

ii. Classify the set of inbred lines into heterotic groups using the HGCAMT, SSR-GD and SNP-GD methods, and assess the effectiveness of the three heterotic grouping methods.

5.2 Materials and methods

5.2.1 Genetic materials

Thirty early maturing maize inbred lines with varying reaction to *Striga* infestation and low-N were used in this study (Table 5.1). The inbred lines were selected based on their performance under *Striga* and low-N environments in the experiments described in chapter 4. The 30 inbred lines were grouped into six sets with each set consisting of five inbred lines. The six sets comprised three sets each of white and yellow endosperm coloured maize. Each inbred line was used as a female parent in one set and a male parent in another set based on the North Carolina Design 2 mating scheme (Comstock and Robinson, 1948). A total of 150 single-cross hybrids (6 sets x 25 hybrids) were developed.

5.2.2 Field procedures

The 150 hybrids and six local hybrid checks were evaluated at Nyankpala in Ghana and Mokwa in Nigeria under artificial *Striga* infestation and optimal growing environments, and also under low-N and optimal growing environments at Kwadaso in Ghana. The experiments were conducted in 2016 and 2017. A 12 x 13 lattice design with two replications were used. Agronomic practices used in this study were similar to those described for similar experiments in Chapter 4 Section 4.2.2.

5.2.3 Data collection

Data collected from the optimal, low N and *Striga*-infested experiments were the same as described in Chapter 4 Section 4.2.3.

Table 5. 1 Description of 30 early maturing maize inbred lines used in North Carolina Design II crosses

Code	Name	Set	Endosperm colour	Reaction to low-N	Reaction to *Striga* infestation
1	TZdEI 283	A	White	Tolerant	Tolerant
2	TZdEI 216	A	White	Tolerant	Tolerant
3	TZEI 378	A	White	Tolerant	Tolerant
4	TZEI 379	A	White	Tolerant	Tolerant
5	TZdEI 69	A	White	Tolerant	Susceptible
6	TZdEI 272	B	White	Tolerant	Tolerant
7	TZdEI 215	B	White	Susceptible	Tolerant
8	TZEI 402	B	White	Tolerant	Tolerant
9	TZEI 3A	B	White	Tolerant	Tolerant
10	TZEI 298	B	White	Susceptible	Tolerant
11	TZdEI 238	C	White	Tolerant	Tolerant
12	TZEI 365	C	White	Tolerant	Tolerant
13	TZEI 376	C	White	Tolerant	Tolerant
14	TZdEI 192	C	White	Tolerant	Tolerant
15	TZdEI 124	C	White	susceptible	Tolerant
16	TZEI 468	D	Yellow	Tolerant	Tolerant
17	TZEI 485	D	Yellow	Tolerant	Tolerant
c18	TZEI 461	D	Yellow	Tolerant	Tolerant
19	TZdEI 40	D	Yellow	Tolerant	Tolerant
20	TZEI 520	D	Yellow	Tolerant	Tolerant
21	TZEI 472	E	Yellow	Tolerant	Tolerant
22	TZEI 456	E	Yellow	Susceptible	Tolerant
23	TZEI 462	E	Yellow	Tolerant	Susceptible
24	TZEI 467	E	Yellow	Tolerant	Tolerant
25	TZEI 127	E	Yellow	Susceptible	Tolerant
26	TZEI 475	F	Yellow	Tolerant	Tolerant
27	TZEI 8	F	Yellow	Tolerant	Tolerant
28	TZEI 470	F	Yellow	Tolerant	Tolerant
29	TZEI 449	F	Yellow	Tolerant	Susceptible
30	TZEI 497	F	Yellow	Tolerant	Tolerant

5.2.4 Statistical analysis

5.2.4.1 Analysis of variance

Analysis of variance involving all the 156 hybrids including the local checks was done for all measured traits for each research condition (optimal, low-N, and *Striga*-infested environments). In the combined analysis of variances, each combination of location and year was treated as test environment. Genotypes were considered as fixed effect while genotype by environment interaction, replication within environment, and block within replication and environment were considered as random effects using PROC GLM in SAS version 9.2 with a RANDOM statement with the TEST option (SAS Institute, 2008). The genotype means were adjusted for block effects, according to the lattice design (Cochran and Cox, 1957). Means were separated using the LSD and Adjusted means estimated with their standard errors. The following statistical model was used for the analysis of variance (ANOVA):

Single environment: $Y_{ijk} = \mu + Rep_i + Block_j(Rep_i) + Entry_k + e_{ijk}$

Where Y_{ijk} is the trait of interest, μ is the mean effect, Rep_i is the effect of the *i*th replicate, $Block_j(Rep_i)$ is the effect of the *j*th incomplete block within the *i*th replicate, $Entry_k$ is the effect of the *k*th entry or genotype, and e_{ijk} is the error associated with the *i*th replication, *j*th incomplete block and kth entry or genotype.

Across environments:

$$Y_{ijkl} = \mu + Env_i + Rep_j(Env_i) + Block_k(Env_i Rep_j) + Entry_l + Env_i \times Entry_l + e_{ijkl}$$

Where Env_i and $Env_i \times Entry_l$ are the effects of the *i*th environment and the environment-by-entry interaction, respectively.

Analysis of variance involving only the 150 test hybrids excluding the local checks was performed separately for all measured traits under each of the three research conditions. Combined analysis of variance was subsequently performed by fitting the general linear model with type III sum of squares for all measured traits using PROC GLM in SAS with a RANDOM statement with the TEST option (SAS Institute, 2008). In North Carolina Design II analysis (NCII), the entry main effect was partitioned into variation due to malewithin-sets, female-within-sets and female-by-male-within-sets interaction. The main effects of male-within-sets and female-within-sets is a measure of the general combining ability (GCA) while the female-by-male-within-sets interaction reflects the specific combining ability (SCA) effect (Hallauer and Miranda, 1988). Approximate F tests (Satterthwaite, 1946) were constructed based on the expectations of mean squares and used to test the male and female within set mean square. The following model was assumed for each year (Singh and Narayanan, 1993):

$$Y_{ijkln} = \mu + s_i + b_{ij} + m_{ik} + f_{i1} + (m\,x\,f)_{ik1} + e_{ijk1n}$$

Where: Y_{ijkln} is the observation made; μ is the overall mean; s_i is the effect of i^{th} set; b_{ij} is the effect of j^{th} replication in i^{th} set; mik is the effect of k^{th} male in i^{th} set; fil is the effect of

l^{th} female in i^{th} set; $(m \times f)_{ikl}$ is the effect of k^{th} male and l^{th} female in the i^{th} set; e_{ijkln} is the error associated with each observation.

The proportionate contribution for each trait was computed as percentage of the sum of squares for the crosses attributed to general combining ability (GCA) and specific combining ability (SCA) as follows:

$$Contribution\ of\ GCA_{male} = \left[\frac{ssm}{(ssm + ssf + ssmf)} x100\right]$$

$$Contribution\ of\ GCA_{female} = \left[\frac{ssf}{(ssm + ssf + ssmf)} x100\right]$$

$$Contribution\ of\ SCA(\%) = \left[\frac{ssmf}{(ssm + ssf + ssmf)} x100\right]$$

Where:

ssm = sum of squares due to males within sets, ssf = sum of squares due to females within sets, ssmf = sum of squares due to male x female within sets interaction,

The relative GCA_{males}, $GCA_{females}$ and SCA effects for grain yield were computed from the adjusted means using the line x tester approach (Singh and Chaudhary, 1985).

$$GCA_{males} = X_j - Y$$

$$GCA_{females} = \bar{X}_i - \bar{Y}$$

$$SCA = \bar{X}_{ij} - \bar{X}_i - \bar{X}_j + \bar{Y}$$

Where:

$\bar{\bar{X}}_j$ = the mean of hybrids with a given male averaged over replicates, environments and females,

$\bar{X}_i$ = themean of hybrids with a given female averaged over replicates, environments and males,

X_{ij} = the mean of a given hybrid averaged over replicates, environments and females,

$\bar{Y}$ = the experimental mean

Standard errors for GCAs effects were calculated as described by Cox and Frey (1984):

$$SE_{GCA} = \left[\frac{MS_{fe}(f-1)}{mfer}\right]^{1/2} \; or \; \left[\frac{MS_{me}(m-1)}{mfer}\right]^{1/2}$$

$$SE_{SCA} = \left[\frac{MS_{fme}(m-1)(f-1)}{mfer}\right]^{1/2}$$

Where,

MS_{fe}, MS_{me} and MS_{fme} are the respective female x environment, male x environment and female x male x environment interaction mean squares and are multiplied by the appropriate proportion of total number of observations (female x male x replicate x environment). T–tests were used to test the significance of the GCA and SCA effects, with t = GCA / SE_{GCA} or SCA / SE_{SCA}, respectively.

The proportion of GCA-male, GCA-female, and SCA for each trait was computed as percentage of the sum of squares for the crosses across research environments. The GCAmales and GCA-females effects for each trait was estimated from the adjusted means (Singh and Chaudhary, 1985) as:

$$Contribution\ of\ GCA_{male} = \left[\frac{ssm}{(ssm + ssf + ssmf)}\ x\ 100\right]$$

$$Contribution\ of\ GCA_{female} = \left[\frac{ssf}{(ssm + ssf + ssmf)}\ x\ 100\right]$$

$$Contribution\ of\ SCA(\%) = \left[\frac{ssmf}{(ssm + ssf + ssmf)}\ x\ 100\right]$$

Where:

ssm = sum of squares due to males within sets, ssf = sum of squares due to females within sets, ssmf = sum of squares due to male x female within sets interaction.

Standard errors for GCAs effects was estimated, GCA-Male and GCA-female effects was tested for significance using two tailed tests as described by Cox and Frey (1984).

Table 5. 2 Expectation of mean squares from the analysis of variance of NCII repeated

over environments

Source of variation	Degrees of freedom	Mean square	Expected mean square
Environment (E)	e-1‡		
Sets (S)	s-1		
S x E	(e-1) (s-1)		
Replications/S/E	es (r-1)		
Block(Replication x E)	re (b-1)		
Males/S	s (m-1)	MS_M	$\sigma^2 + r\sigma^2_{emf} + rf\sigma^2_{em} + re\sigma^2_{mf} + ref\sigma^2_{m}$
Females/S	s (f-1)	MS_F	$\sigma^2 + r\sigma^2_{emf} + rm\sigma^2_{ef} + re\sigma^2_{mf} + rem\sigma^2_{f}$
Males x females/S	s (m-1) (f-1)	MS_{MF}	$\sigma^2 + r\sigma^2_{emf} + re\sigma^2_{mf}$
E x Males/S	s (e-1) (m-1)	MS_{EM}	$\sigma^2 + r\sigma^2_{emf} + rf\sigma^2_{em}$
E x Females/S	s (e-1) (f-1)	MS_{EF}	$\sigma^2 + r\sigma^2_{emf} + rm\sigma^2_{ef}$
E x Males x Females/S	s (e-1) (m-1) (f-1)	MS_{EMF}	$\sigma^2 + r\sigma^2_{emf}$
Pooled error	es (r-1) (mf-1)	MS_E	σ_2
Total	esrmf-1		

‡ e, s, r, m, and f refer to the number of environments, sets within an environment, replications, number of males and number of females, respectively.

5.2.4.2 Heterotic grouping

Heterotic grouping based on GCA of multiple traits (HGCAMT) proposed by BaduApraku *et al.* (2013, 2015) was used to assign the 30 inbred lines into heterotic groups under *Striga* infestation, low-N, optimal growing conditions, and across research environments. The heterotic groupings of the inbred lines was achieved by standardizing the GCA effects with a mean of zero and standard deviation of 1 for all traits that had significant genotypic mean squares and GCA under the different research conditions, namely; optimal, low-N, *Striga*-infested and across research environments. The following statistical model was used:

$$Y = \sum_{i=1}^{n} \left(\frac{(Y_i - Y_i)}{S} \right)$$

Where Y is HGCAMT, which is the genetic value measuring relationship among genotypes based on the GCA of multiple traits *i* to *n*; Y_i is the individual GCA effect of genotypes for trait *i*, Y_i is the mean of GCA effects across genotypes for trait *i*, S is the standard deviation of the GCA effects of trait *i* and e_{ij} is the residual of the model associated with the combination of inbred *i* and trait *j*

The standardized GCA effects were converted to Euclidean distance using PROC DISTANCE procedure in SAS and subsequently subjected to Ward's minimum variance cluster analysis using PROC CLUSTER procedure in SAS (SAS Institute, 2008).

For the SNP and SSR marker-based methods of heterotic grouping, the genetic distances (GD) estimated from SNP and SSR markers were used to assign the 30 inbred lines into heterotic groups following the GD measurement and clustering analyses described in Chapter 3 section 3.3.2.

The efficiency of the three heterotic grouping methods were compared based on their breeding efficiencies at each and across the three research environments (Fan *et al.*, 2009). This was done by arranging the 150 hybrids from the highest to the lowest performer based on grain yield under low-N, *Striga* infestation, optimal growing conditions, and across environments. The total number of hybrids for each method was placed into two major groups: intergroup and intragroup crosses. Subsequently, the total number of hybrids within each of the two major groups were divided into three groups: high-yielding hybrids (Yield Group 1 with a mean grain yield ranking among the top 50 lines), intermediate hybrids (Yield Group 2 with a grain yield between the 51st and 100th lines), and lowyielding hybrids (Yield Group 3 with a mean grain yield between 101st and 150th lines). In the present study, we defined breeding efficiency as the average of the proportion of total inter-heterotic group hybrids that is due to superior high-yielding inter-heterotic group hybrids plus the proportion of total low-yielding intra-heterotic group hybrids that is due to the low-yielding intra-heterotic group hybrids. For this purpose, Groups 1 and 3 were considered the high-yielding and low-yielding groups, respectively.

The breeding efficiency (BE) was calculated as follows:

$$Breeding\ Efficiency = \frac{\left[\frac{HY\ INTERGH}{TN\ INERGH}\ x\ 100\right] + \left[\frac{LY\ INTRAGH}{TN\ INTRAGH}\ x\ 100\right]}{2}$$

Where HYINTERGH is the number of high-yielding inter-heterotic group hybrids; TNINTERGH is the total number of inter-heterotic group hybrids, LYINTRAGH is the number of low-yielding intra-heterotic group hybrids; and TNINTRAGH is the total number of intra-heterotic group hybrids.

5.3 Results

5.3.1 Genetic analysis of performance of early maturing maize inbred lines under contrasting environments

Under each of the three research environments (Tables 5.3 to Table 5.5), there were significant differences among the genotypes, environments and GEI effects for almost all measured traits except for differences observed for ASI, which was not significant for genotype and GEI under optimal conditions and *Striga*-infested environments. Similarly, no significant differences were observed for GEI mean squares for number of emerged *Striga* plants at 8 and 10 WAP under *Striga* infestation (Table 5.4), and for ear aspect for genotype and GEI under low-N environments (Table 5.5).

Results from the combined analyses of variances (ANOVA) of the hybrids including the local checks showed significant genotype (G), environment (E) and GEI effects for almost all measured traits except for genotype and GEI for anthesis-silking interval (ASI) (Table 5.6).

Table 5. 3

Mean squares for grain yield and agronomic traits of 156 early maturing single-cross hybrids and local checks under optimal growing conditions at Kwadaso, Nyankpala and Mokwa in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Anthesissilking interval	Plant height	Ear height	Stalk lodging	Plant aspect	Ear aspect	Ears per plant
Environment (E)	3	128930826.60**	4651.21**	2672.88**	739.41**	25973.74**	3878.79**	128.68**	868.72**	836.18**	1.57**
Replication (E)	4	11097779.10**	16.16*	12.92*	0.54^{ns}	978.68*	493.41**	3.46*	11.93**	2.77**	0.15^{ns}
Block (E*REP)	96	1537262.10*	7.50**	8.40**	0.83*	421.30**	137.96**	1.01*	0.93**	0.65**	0.07^{ns}
Genotype (G)	155	3350625.40**	11.68**	13.43**	0.66^{ns}	1914.26**	292.32**	1.21**	1.59**	1.03**	0.16**
G x E	465	1584497.60**	5.18**	6.27**	0.65^{ns}	369.54**	107.02**	0.93*	0.75**	0.47**	0.12**
Error	524	975192.00	2.83	3.27	0.58	192.64	61.03	0.68	0.38	0.30	0.07

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non- significant; REP, replication

Table 5. 4 agronomic trai

Mean squares for grain yield and ts of 156 early maturing single-cross hybrids and local checks under *Striga* infestation at Nyankpala, Manga and Mokwa in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Anthesissilking interval	Ear aspect	Ears per plant	STRRAT1	STRRAT2	STRCO1	STRCO2
Environment (E)	3	47069185.30**	2153.65**	1890.76**	22.03**	439.31**	9.81**	1567.83**	1915.68**	0.20ns	65.98**
Replication (E)	4	2438688.10**	16.49*	19.76*	0.19ns	7.46**	0.11*	3.07*	23.72**	20.33**	21.60**
Block (E x REP)	96	763209.50**	10.48**	13.49**	0.27ns	2.09**	0.05*	2.08**	3.36**	2.16*	1.23*
Genotype (G)	155	693210.70**	14.28**	11.36**	0.21ns	1.86**	0.07**	1.37**	1.62**	2.77*	2.35**
G x E	465	461059.90*	6.21*	9.28*	0.21ns	1.33**	0.05*	1.04**	1.04*	1.29ns	0.82 ns
Error	524	332645.7	4.89	6.71	0.21	0.92	0.04	0.65**	0.8	1.39	0.82

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non significant; ; REP, replication; STRRAT1, *Striga* damage rating at 8 weeks after planting; STRRAT2, *Striga* damage rating at 10 weeks after planting; STRCO1, *Striga* emergence count at 8 weeks after planting; STRCO2, *Striga* emergence count at 8 weeks after planting

Table 5. 5 agronomic trai

Mean squares for grain yield and ts of 156 early maturing single-cross hybrids and local checks under low soil nitrogen at Kwadaso in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Plant height	Ear height	Stalk lodging	Plant aspect	Ear aspect	Ears per plant	Stay green
Environment (E)	1	58582369.30**	1158.90**	1127.50**	11926.95**	956.84*	1.20^{ns}	60.32**	0.00^{ns}	1.72**	30.00**
Replication (E)	2	5435742.50**	74.46**	99.00**	3599.42**	2471.05**	6.96*	13.34**	0.52^{ns}	0.024^{ns}	17.87**
Block (E x REP)	48	1621685.80**	24.16**	27.92**	803.45**	235.70**	1.96*	0.56**	0.47**	0.07^{ns}	2.14**
Genotype (G)	155	1015711.90**	8.55*	12.70*	779.34**	160.48**	1.73*	0.33**	0.24^{ns}	0.07*	1.51**
G x E	155	622621.60**	6.22^{ns}	10.96*	335.93*	96.03*	1.26^{ns}	0.29**	0.17^{ns}	0.05^{ns}	0.20^{ns}
Error	262	362399.7	5.65	8	222.49	68.22	1.08	0.24	0.19	0.05	0.61

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non significant; REP, replication

Table 5. 6 agronomic trai ts of 156 early maturing single-cross hybrids and local checks

Mean squares for grain yield and

across optimal, *Striga*-infested and low -N environments in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to anthesis	Anthesis-silking interval	Plant height	Ear height	Stalk lodging	Plant aspect	Ear aspect	Ears per plant
Environment (E)	9	196252488.00**	6182.77**	3104.84**	544.54**	66129.84**	28792.69**	215.55**	659.99**	488.60**	6.82**
Replication (E)	10	6501735.00**	27.95**	32.87**	2.48ns	1456.88**	850.48**	3.98**	9.51**	4.20**	0.11*
Block (E x REP)	240	1244526.00**	12.02**	14.34**	2.86*	514.61**	152.56**	1.20**	1.12**	1.19**	0.06ns
Genotype (G)	155	3101254.00**	21.89**	21.51**	2.46ns	2795.56**	405.55**	1.92**	2.30**	1.83**	0.14**
G x E	1395	965112.00**	5.91**	8.18**	2.46ns	335.06**	91.32**	0.90*	1.00**	0.76**	0.08**
Error	1310	595615.00	4.22	5.59	2.34	197.99	63.07**	0.75	0.51	0.52	0.05

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non-significant; REP, replication

Table 5. 7 **agronomic trai**

Partitioning of the genotypic mean squares into its components revealed significant differences in mean squares of environments (E) for all measured traits except for anthesissilking interval under optimal conditions (Table 5.7). The GCAm (GCA effects of inbred used as a male parent), GCAf (GCA effects of inbred used as a female parent) and SCA were significant for all measured traits except for anthesis-silking interval for GCAm, GCAf, and anthesis-silking interval and root lodging for SCA. The interactions between environment and GCAm were significant for all measured traits except for anthesis-silking interval. Furthermore, SCA x E interaction effect was significant for all measured traits, while GCAf x E interaction was significant for all measured traits except for root and stalk lodgings (Table 5.7).

The mean squares due to set were significant for all measured traits except for anthesissilking interval, root lodging and husk cover under *Striga*-infested environments. Similarly, the differences observed among environments were significant for all measured traits except for number of emerged *Striga* plants at 8 WAP (Table 5.8). The GCAm mean squares for anthesis-silking interval, ear height, stalk lodging and husk cover as well as GCAf mean squares for anthesis-silking interval and stalk lodging were not significant. The SCA effects were significant for all measured traits except for anthesis-silking interval, stalk lodging and husk cover (Table 5.8). The GCAm x E interaction effect was significant for husk cover, ear aspect, ears per plant, number of emerged *Striga* plants at 8 and 10 WAP, while GCAf x E interaction effects were significant for grain yield, days to anthesis, days to silking, root lodging, husk cover, plant aspect, ear aspect, *Striga* damage syndrome rating at 8 and 10 WAP (Table 5.8). The interaction between SCA and environment was

significant for all measured traits except for anthesis-silking interval, ear height, husk cover, *Striga* damage syndrome rating at 8 WAP, and for number of emerged *Striga* plants at 8 and 10 WAP (Table 5.8).

Under low-N, the differences among environments were significant for all measured traits except for anthesis-silking interval, root lodging and stalk lodging (Table 5.9). The differences observed among sets were significant for grain yield, plant height, ear height, husk cover, plant aspect, ear aspect, ears per plant and stay green characteristic. The interaction between environment and set was significant for grain yield, plant height, husk cover, and plant aspect (Table 5.9). The GCAm and GCAf effects were significant for all measured traits except for anthesis-silking interval, plant aspect and ear aspect for GCAm, and anthesis-silking interval, husk cover, plant aspect, ear aspect and ears per plant for GCAf. The SCA effect was significant for grain yield, plant height, ear height, root lodging and stay green characteristic. The interaction between environment and GCAm was significant for days to silking, husk cover, plant aspect and stay green characteristic, while GCAf x E was significant for grain yield, days to anthesis, days to silking, ear height and stay green characteristic. Furthermore, SCA x E were significant for all measured traits except for grain yield, plant height and stay green characteristic (Table 5.9). Across optimal growing conditions, *Striga*-infested and low-N environments, the differences among environments were significant for all measured traits (Table 5.10). Similarly, the mean squares due to set, set x E, GCAm, GCAf, SCA, GCAm x E, GCAf x E and SCA x E were significant for all measured traits except for anthesis-silking interval (Table 5.10).

Table 5. 7 Mean squares derived from the analysis of variance for grain yield and agronomic traits of the 150 single-cross hybrids under optimal growing conditions at Nyankpala, Kwadaso and Mokwa in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Plant height	Ear height	Stalk lodging	Plant aspect	Ear aspect	Ears per plant
Environment (E)	3	115159309.20**	4466.41**	2588.80**	24827.87**	4028.33**	121.96**	830.88**	786.93**	1.43**
Set	5	9415440.80**	35.41**	39.41**	26721.29**	1615.15**	0.95ns	11.75**	8.01**	0.17*
E x Set	15	2016314.10*	8.74**	8.50*	715.28**	130.08*	1.23*	0.87*	0.49ns	0.12*
REP (E x Set)	20	847607.70ns	3.07ns	3.172ns	297.90*	52.55ns	0.77ns	0.41ns	0.18ns	0.13*
Block (E x REP)	96	1526045.00*	6.94**	7.40**	417.74**	141.66**	0.92*	0.97**	0.66**	0.07ns
GCA-Male(Set)	24	3449292.50**	16.70**	19.33**	1665.97**	271.18**	1.76**	0.93*	0.98**	0.22**
GCA-Female(Set)	24	4688082.70**	17.71**	21.02**	1797.22**	484.18**	1.53*	1.73**	1.25**	0.23**
SCA(Set)	96	2481527.20**	6.87**	7.87**	549.83**	131.25**	1.06*	1.09**	0.59**	0.12*
E x GCA-Male(Set)	72	1349720.60*	6.80**	7.86**	335.27**	108.71*	0.91*	0.88**	0.58**	0.10*
E x GCA-Female(Set)	72	1703657.40*	6.03**	6.68**	390.85**	138.28**	0.84ns	0.70*	0.45*	0.14**
E x SCA(Set)	288	1521403.70**	4.04*	5.01**	344.79**	91.04**	0.93*	0.67**	0.43*	0.12**
Error	480	975007	2.78	3.15	180.54	59.27	0.68	0.38	0.30	0.07

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non significant; GCA, general combining ability; SCA, specific combining ability; REP, replication

Table 5. 8 Mean squares derived from analysis of variance for grain yield and agronomic traits of the 150 single-cross hybrids under artificial *Striga*-infested environments at Nyankpala, Manga and Mokwa in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Plant height	Ear height	Stalk lodging
Environment (E)	3	45253715.30**	2007.65**	1827.14**	69452.55**	4624.55**	316.83**
Set	5	2537531.50**	21.03*	27.40*	6836.23**	760.45**	1.78*
E x Set	15	569442.60*	10.26*	11.90*	560.48*	108.26ns	0.65ns
REP (E x Set)	20	549732.80*	5.10ns	4.29ns	120.23ns	46.63ns	0.72ns
Block (E x REP)	96	772888.90**	10.23**	12.87**	427.12**	115.41**	0.99*
GCA-Male(Set)	24	741937.20*	23.49**	19.48**	930.75**	89.23ns	0.89ns
GCA-Female(Set)	24	1002635.70**	18.41**	11.60*	962.94**	212.62**	0.88ns
SCA(Set)	96	541397.90**	10.79**	9.23*	501.63**	137.13**	0.81ns
E x GCA-Male(Set)	72	376159.10ns	5.81ns	9.07ns*	146.91ns	43.73ns	0.54ns
E x GCA-Female(Set)	72	608112.80*	6.63*	9.71*	260.05ns	53.88ns	0.81ns
E x SCA(Set)	288	442171.40*	5.96*	8.41*	266.31*	67.06ns	0.79*
Error	480	330203.4	4.85	6.91884	200.5	64.6	0.64

*, **, Significant at 0.05 and 0.01 probability levels, respectively, and ns, non- significant; GCA, general combining ability; SCA, specific combining ability; REP, replication.

Table 5.8 Cont'd

Source of variation	DF	Plant aspect	Ear aspect	Ears per plant	*Striga* damage syndrome rating		*Striga* emergence count	
					@ 8 WAP	@ 10 WAP	@ 8 WAP	@ 10 WAP
Environment (E)	3	771.40**	406.07**	9.21**	1461.83**	1778.24**	0.27^{ns}	64.41**
Set	5	11.68**	12.98**	0.36**	6.79**	7.23**	4.64*	3.37*
E x Set	15	1.95*	2.03*	0.06^{ns}	2.28**	2.30*	1.60^{ns}	1.02^{ns}
REP (E x Set)	20	0.82^{ns}	0.82^{ns}	0.03^{ns}	0.52ns	0.98^{ns}	0.91^{ns}	0.84^{ns}
Block (E x REP)	96	1.57**	2.11**	0.05*	2.23**	3.41**	2.02*	1.15*
GCA-Male (Set)	24	2.40**	1.96*	0.08*	1.83**	1.40*	3.37*	2.99**
GCA-Female (Set)	24	1.91*	1.87*	0.06*	2.02**	2.69**	2.23*	1.84*
SCA (Set)	96	1.75**	1.46*	0.05*	0.89*	1.19*	2.32*	1.98**
E x GCA-Male (Set)	72	1.30*	1.16^{ns}	0.0$_{4ns}$	1.25**	1.12*	0.94^{ns}	0.82^{ns}
E x GCA-Female (Set)	72	2.09**	1.53*	0.04^{ns}	1.47**	1.23*	1.45^{ns}	0.74^{ns}
E x SCA (Set)	288	1.32**	1.18*	0.05*	0.83*	0.88^{ns}	1.26^{ns}	0.80^{ns}
Error	480	0.76	0.91	0.04	0.62	0.78	1.4	0.84

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non significant; GCA, general combining ability; SCA, specific combining ability; REP, replication; WAP, weeks after planting

Table 5. 9 Mean squares derived from analysis of variance for grain yield and agronomic traits of the 150 single-cross hybrids under low-N environments at Kwadaso in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Plant height	Ear height	Stalk lodging	Plant aspect	Ears per plant	Stay green
Environment (E)	1	56151421.20**	1054.34**	1023.82**	10293.54**	765.87*	1.06^{ns}	56.90**	1.63**	14.47**
Set	5	3448488.28**	10.27^{ns}	10.14^{ns}	6885.76**	539.25**	2.23^{ns}	2.09**	0.13*	1.34*
E x Set	5	2027960.34**	7.79^{ns}	9.52^{ns}	1242.53**	142.33^{ns}	1.69^{ns}	1.28**	0.02^{ns}	0.51^{ns}
REP (E x Set)	10	354738.22^{ns}	4.33^{ns}	5.48^{ns}	182.63^{ns}	54.93^{ns}	2.35*	0.28ns	0.08^{ns}	0.23^{ns}
Block (E x REP)	48	1580401.07**	23.61**	27.75**	743.40**	224.027**	1.97*	0.55**	0.06^{ns}	1.59**
GCA-Male (Set)	24	1099894.80**	10.27*	15.08*	739.52**	181.36*	3.07**	0.32^{ns}	0.09*	1.61**
GCA-Female (Set)	24	1891256.15**	16.04**	20.05*	1134.05**	265.98**	2.92**	0.28^{ns}	0.07^{ns}	0.73*
SCA (Set)	96	635867.34*	6.42^{ns}	10.10^{ns}	376.88*	108.08*	1.27^{ns}	0.25^{ns}	0.06^{ns}	0.76**
E x GCA-Male (Set)	24	429290.67^{ns}	7.64^{ns}	15.01*	352.43^{ns}	72.69^{ns}	1.36^{ns}	0.37*	0.04^{ns}	0.76*
E x GCA-Female (Set)	24	889135.25*	9.24*	13.90*	181.57^{ns}	152.10*	0.97^{ns}	0.22^{ns}	0.05^{ns}	0.87*
E x SCA (Set)	96	540604.59*	4.77^{ns}	8.79^{ns}	311.44*	88.40^{ns}	1.27^{ns}	0.25^{ns}	0.06^{ns}	0.59*
Error	240	366531.9	5.6	7.9	230.09	70.34	1.06	0.23	0.05	0.38

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non significant; GCA, general combining ability; SCA, specific combining ability; REP, replication

Table 5. 10 Mean squares derived from combined analysis of variance for grain yield and agronomic traits of the 150 single-cross hybrids across optimal, low-N and *Striga*-infested environments in 2016 and 2017

Source of variation	DF	Grain yield	Days to anthesis	Days to silking	Plant height	Ear height	Stalk lodging	Plant aspect	Ear aspect	Ears per plant
Environment (E)	9	179855731.00**	5873.88**	2976.85**	61898.92**	26746.67**	202.06**	625.78**	454.72**	6.38**
Set	5	12940872.00**	52.01**	54.79**	36680.73**	2371.16**	2.91*	23.82**	20.018**	0.52**
E x Set	45	1361733.00**	8.79**	10.30*	985.76**	155.91**	1.04*	1.27**	1.14**	0.08*
REP (E x Set)	50	629884.00ns	4.13ns	4.078ns	203.78ns	50.66ns	1.07*	0.55ns	0.44ns	0.08*
Block (E x REP)	240	1235654.00**	11.59**	13.66**	486.62**	147.63**	1.16**	1.13**	1.21**	0.06ns
GCA-Male (Set)	24	3361846.00**	36.61**	37.57**	2771.16**	406.75**	2.94**	1.71**	1.29*	0.19**
GCA-Female (Set)	24	5577354.00**	37.34**	34.28**	3165.21**	760.62**	2.92**	1.95**	1.70**	0.18**
SCA (Set)	96	1818905.00**	12.25**	11.71**	738.51**	177.21**	1.47**	1.28**	1.18**	0.10**
E x GCA-Male (Set)	216	837802.00*	6.65**	9.16**	262.71*	73.98*	0.93*	0.99**	0.80**	0.08*
E x GCA-Female (Set)	216	1089969.00***	6.87**	9.01**	316.87**	103.11**	0.93*	1.17**	0.88**	0.08**
E x SCA (Set)	864	915972.00**	5.17*	7.19**	315.47**	84.81**	0.90*	0.89**	0.68**	0.08**
Error	1200	595390	4.17	5.60762	198.43	63.61	0.74	0.5	0.52	0.05

*, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, non - significant; GCA, general combining ability; SCA, specific combining ability; REP, replication

5.3.2 Relative contributions of combining ability effects

The relative importance of GCA mean squares over SCA mean squares under optimal, lowN, *Striga*-infested and across environments are presented in Table 5.11. Under optimal environments, the total contributions of GCA (GCAm plus GCAf) sum of squares to the total variation among hybrids ranged from 25.81% to 46.52%, while those of SCA ranged from 17.79% to 64.39% (Table 5.11). The contributions of GCA sum of squares to the total variation among hybrids were larger than those of SCA for days to silking, days to anthesis, ear and plant heights, while the contribution of SCA sum of square to the total variation among hybrids were larger than those of GCA for grain yield, root lodging, stalk lodging, anthesis-silking interval, plant aspect and husk cover. The contribution of GCA and SCA to the variation among the hybrids were approximately equal for ears per plant and ear aspect (Table 5.11).

Under *Striga*-infested environments, the total contributions of GCA sum of squares to the total variation among hybrids ranged from 28.15% to 45.44%, while those of SCA ranged from 35.33% to 64.61% (Table 5.11). Except for *Striga* damage syndrome rating at 8 WAP, the contribution of SCA to genotypic variation among the hybrids for grain yield and the other traits measured under *Striga* infestation were greater than the contribution of GCA. The SCA accounted for about 64.61% of the sum of squares for anthesis–silking interval, 58.74% for stalk lodging, 57.37% for root lodging, 55.15% for husk cover, 51.98% for *Striga* emergence count at 10 WAP, 51.90% for *Striga* emergence count at 8 WAP, 51.46% for ear height and 50.35% for days to silking. Generally, the contribution of GCAf was higher than GCAm for grain yield, anthesis–silking interval, stalk lodging, root lodging, husk cover and *Striga* damage syndrome rating at 10 WAP, while the GCAm was larger

than GCAf sum of squares for number of emerged *Striga* plants at 8 and 10 days to silking, ears per plant and days to anthesis. (Table 5.11).

General combining ability (GCA) accounted for 32.85 to 51.33 % of the total variation among hybrids for grain yield (45.60%), plant height (37.22%) and stalk lodging (53.55%) under low-N (Table 5.11). Specific combining ability (SCA) accounted for 47.02 to 65.95% of the total variation among hybrids for plant aspect (47.02%), ear aspect (54.71%), ears per plant (53.38%), stay green characteristic (49.59%), days to silking (49.26%) and anthesis–silking interval (65.95%). The contribution of GCA and SCA to genotypic sum of squares for days to anthesis, ear height, root lodging and husk cover was about the same magnitude under low-N (Table 5.11). Generally, the contribution of GCAf was higher than GCAm for grain yield, days to anthesis, days to silking, plant height, ear height, husk cover and ear aspect, while the GCAm was larger than GCAf sum of squares for anthesis–silking interval, plant aspect, husk cover and ears per plant under low-N. Similar magnitudes of GCAm and GCAF sum of squares were obtained for root lodging, stalk lodging, plant aspect and stay green characteristic (Table 5.11).

Across research environments, grain yield, days to anthesis, days to silking, plant height and ear height had greater GCA sum of squares than SCA sum of squares. On the contrary, the SCA effect was greater than GCA effects for anthesis–silking interval, stalk lodging, husk cover, plant aspect, ear aspect and ears per plant across environments (Table 5.11).

Table 5. 11 Proportion of the sum of squares for crosses attributable to general combining ability (GCA) and specific combining ability (SCA) for grain yield and agronomic traits of early maturing inbred lines under optimal, low-N, *Striga*-infested environments and across environments in 2016 and 2017

Trait	Optimal			*Striga*-infested			Low-N			Across environments		
	GCA		SCA	GCA		SCA	GCA		SCA	GCA		SCA
	Male	Female		Male	Female		Male	Female		Male	Female	
Grain yield	15.94	21.66	45.87	16.57	22.40	48.37	16.77	28.83	38.77	16.78	27.85	36.33
Days to anthesis	22.15	23.48	36.45	25.48	19.96	46.79	18.60	29.04	46.45	25.89	26.41	34.65
Days to silking	22.28	24.24	36.28	26.56	15.82	50.35	18.38	24.45	49.26	27.05	24.68	33.72
Anthesis–silking interval	14.62	14.08	64.39	9.66	18.48	64.61	16.88	6.97	65.95	9.24	16.32	64.66
Plant height	13.48	14.54	17.79	16.39	16.95	35.33	14.69	22.53	29.95	15.35	17.53	16.36
Ear height	14.36	25.65	27.81	8.37	19.95	51.46	17.50	25.66	41.71	15.53	29.04	27.06
Root lodging	22.43	19.48	54.09	14.90	21.74	57.37	25.28	26.05	49.71	23.67	23.49	47.23
Stalk lodging	20.94	12.11	52.60	16.24	16.08	58.74	27.43	26.12	45.60	22.20	19.70	48.64
Husk cover	12.94	12.87	32.64	18.15	21.00	55.15	21.66	11.19	32.85	11.54	12.84	32.09
Plant aspect	9.07	16.88	42.24	16.40	13.04	47.83	15.00	12.89	47.02	11.47	13.08	34.55
Ear aspect	14.82	18.77	35.70	16.31	15.55	48.46	8.16	19.08	54.71	10.84	14.32	39.32
Ears per plant	21.61	22.96	47.87	19.31	14.16	49.28	19.77	14.77	53.38	21.26	19.81	46.34
Stay green characteristic							17.91	17.84	49.59			
Striga damage syndrome rating at 8 weeks after plant				20.69	22.86	40.16						
Striga damage syndrome rating at 10 weeks after plant				13.37	25.66	45.40						
Number of emerged *Striga* plants at 8 weeks after plant				18.82	12.43	51.90						
Number of emerged *Striga* plants at 10 weeks after plant				19.70	12.13	51.98						

5.3.3 General combining ability effects

Presented in Tables 5.12 to 5.15 are the GCA effects of the inbred lines under optimal growing conditions, *Striga* infestation, and low-N and across environments. Under optimal growing conditions, the inbred lines TZdEI 40, TZdEI 124, TZEI 127, TZdEI 192, TZdEI 215 and TZEI 449 showed significant positive GCAf effect for grain yield, while TZEI 8, TZdEI 40 and TZEI 127 had significant positive GCAm effects for grain yield (Table 5.12). The inbred lines TZEI 8, TZdEI 69, TZdEI 124 had both significant negative GCAf and GCAm effects for days to anthesis. The inbred lines TZEI 449, TZEI 462 and TZdEI 40 showed significant negative GCAf effects for days to anthesis. The inbred lines TZEI 8 and TZdEI 124 had both significant negative GCAf and GCAm effects for days to silking. Significant and negative GCAf and GCAm effects for plant aspect were obtained by TZdEI 40. The inbred lines TZEI 127 and TZdEI 215 had significant negative GCAf effects for plant aspect (Table 5.12). In contrast, a significant negative GCAf for ear aspect was obtained by TZdEI 40, TZEI 127 and TZdEI 272, while TZdEI 124 and TZEI 497 obtained significant negative GCAm effects. The inbred lines TZdEI 192 and TZEI 461, and TZdEI 272 and TZEI 475 had significant positive GCAf and GCAm effects, respectively, for ears per plant (Table 5.12).

Out of the 30 inbred lines tested in *Striga*-infested environments, only TZdEI 124 and TZEI 127 had significant positive GCAf effects for grain yield (Table 5.13). The inbred lines TZdEI 40, TZEI 127, TZdEI 216 and TZEI 470 had significant positive GCAm effects for grain yield. The inbreds, TZdEI 40, TZEI 127, TZdEI 216, and TZEI 470 had significant positive effects for grain yield (Table 5.13). Inbred lines TZdEI 272 had significant

negative GCAm effect for number of emerged *Striga* plants at 8 and 10 WAP. Similarly, inbred line TZdEI 216 had significant negative GCAm effect for *Striga* damage syndrome rating and number of emerged *Striga* plants at 8 WAP as well as significant negative GCAm and GCAf effects for *Striga* damage syndrome rating at 10 WAP. The inbred lines TZdEI 216 and TZEI 402 had significant negative GCAm for *Striga* damage syndrome rating at 8 WAP (Table 5.13). Inbred lines TZEI 379 and TZEI 468 had significant negative GCAf effects for *Striga* emergence count at 8 WAP. The inbred lines TZdEI 216 and TZEI 470 had significant negative GCAm effects for *Striga* damage syndrome rating at 10 WAP, while TZEI 127, TZdEI 192 and TZdEI 216 had significant negative GCAf effects for *Striga* damage syndrome rating at 10 WAP. A significant negative GCAm effects for *Striga* emergence count at 8 WAP was obtained by TZEI 298, TZEI 378, TZEI 461, TZEI 462, TZEI 470 and TZEI 472, whereas TZEI 379 and TZEI 468 had significant negative GCAf effects for the same trait. The inbred line TZdEI 192 had significant negative GCAf and GCAm effects for *Striga* emergence count at 10 WAP. The GCAf effect for *Striga* emergence count at 10 WAP was significant and negative for TZdEI 192, TZEI 379 and TZEI 468, while TZdEI 272, TZEI 378, TZEI 462 and TZEI 470 had significant and negative GCAm effects. The only inbred lines with significant positive GCAf effects for ears per plant were TZEI 127 and TZEI 485. A significant and positive GCAm effects for ears per plant was obtained by TZEI 8. TZEI 520 was the only hybrid with a significant negative GCAf effect (Table 5.13).

Under low-N environments, inbred lines TZEI 127, TZdEI 192, TZEI 485 and TZdEI 272 showed significant negative GCAf and GCAm effects for stay green characteristic. A

significant negative GCAf effects were also obtained by TZEI 8, TZdEI 69, TZdEI 215, TZEI 365, TZEI 449 and TZEI 462 for stay green characteristic, whereas TZdEI 283, TZEI 461 and TZEI 470 obtained significant negative GCAm effects. The inbred lines TZdEI 192 and TZEI 449 had significant positive GCAf effects for grain yield, while TZdEI 124 and TZdEI 215 had significant positive GCAm effects for grain yield (Table 5.15). The GCAf effect for days to anthesis was significant and negative for only TZEI 468, while TZEI 298 had significant positive GCAm for ears per plant.

Across the contrasting environments, TZdEI 40, TZdEI 124, TZEI 127 and TZdEI 215 exhibited significant positive GCAf and GCAm effects for grain yield. In contrast, inbred lines TZEI 449, TZdEI 192 and TZdEI 272 had positive GCAf effects for grain yield, whileTZEI 8 and TZdEI 216 had significant positive GCAm effects for grain yield (Table 5.15). Similarly, significant negative GCAm and GCAf effects for days to anthesis were showed by TZEI 8, TZdEI 69 TZEI 468 and TZdEI 124. The inbred lines TZdEI 215, TZdEI 40, TZEI 456 and TZEI 475 exhibited significant negative GCAf for days to anthesis, while TZEI 461, TZEI 467 and TZEI 470 exhibited significant negative GCAm effect for days to anthesis (Table 5.15). The inbred lines TZEI 8, TZdEI 124 and TZEI 456 had significant negative GCAf and GCAm effects for days to silking. Significant and negative GCAf effect for days to silking were obtained by TZdEI 40 and TZEI 475, while TZdEI 69 obtained significant negative GCAm effect for days to silking. The inbred Ines TZdEI 40 and TZEI 127 had significant and negative GCAf and GCAm effects for plant aspect. Similarly, TZdEI 40 and TZEI 127 had significant negative GCAf and GCAm effects for ear aspect, while TZdEI 124 obtained significant negative GCAf for ear aspect,

and TZdEI 272 obtained a significant negative GCAm effect for the same trait. The inbred lines TZEI 8 and TZdEI 272 obtained significant positive GCAm and GCAf effects for ears per plant. The inbred lines TZEI 127 and TZdEI 192 had significant positive GCAf effects for ears per plant, while TZEI 475 had significant and positive GCAm effect for ears per plant (Table 5.15).

Table 5. 12

General combining ability effects of inbred lines for grain yield and other traits under optimal growing conditions

Inbred	Grain yield		Days to anthesis		Days to silking		ASI		Plant aspect		Ear aspect		Ears per plant	
lines	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm
TZEI 3A	-232.58	1.57	-0.42	-0.41	-0.46	-0.58	-0.03	-0.05	0.09	0.04	0.14	-0.09	-0.04	-0.05
TZEI 8	1.96	446.32*	-1.36*	-1.24*	-1.18*	-1.37*	0.07	-0.04	0.27*	0.06	-0.02	0.06	0.06	-0.01
TZdEI 40	790.67*	909.59**	-1.25*	-0.18	-1.41*	-0.33	-0.04	-0.04	-0.55*	-0.30*	-0.36*	-0.24*	0.01	0.07
TZdEI 69	330.56	27.40	-1.03*	-0.95*	-0.99*	-0.79	0.00	0.05	0.02	0.00	-0.15	0.00	0.02	-0.03
TZdEI 124	416.11*	316.51	-0.92*	-1.27*	-1.23*	-1.30*	-0.06	-0.01	0.24	-0.16	-0.01	-0.40*	-0.01	0.04
TZEI 127	436.73*	583.5*	-0.06	0.06	-0.10	0.05	0.00	-0.02	-0.39*	-0.27	-0.38*	-0.17	0.08	0.08
TZdEI 192	430.83*	-232.55	0.42	0.47	0.40	0.44	-0.02	0.01	-0.05	-0.01	0.03	0.14	0.22*	0.01
TZdEI 215	596.28*	250.93	-0.59	0.54	-0.62	0.66	0.00	0.01	-0.33*	-0.07	-0.17	-0.04	-0.01	0.06
TZdEI 216	-45.26	177.40	0.25	-0.43	0.15	-0.56	-0.01	-0.04	-0.03	-0.07	0.14	0.01	-0.02	0.00
TZdEI 238	-218.35	-13.70	0.03	-0.20	0.13	-0.36	0.01	-0.03	-0.05	-0.16	0.06	-0.01	-0.11	-0.01
TZdEI 272	372.17	92.16	0.04	-0.16	-0.08	-0.26	0.00	0.00	0.03	0.09	-0.24*	-0.13	0.10	0.15*
TZdEI 283	142.14	-230.59	0.60	0.42	0.81*	0.29	0.04	-0.03	0.00	-0.09	0.03	-0.07	-0.04	0.02
TZEI 298	-360.30	-214.02	0.62	0.24	0.76	0.16	0.03	-0.01	-0.18	0.01	0.21	0.08	-0.02	-0.10
TZEI 365	-338.53	-312.90	0.02	0.80*	0.03	0.99*	0.01	0.03	-0.07	0.35*	-0.12	0.26*	-0.04	0.00
TZEI 376	-290.08	242.64	0.45	0.20	0.66	0.23	0.07*	0.01	-0.06	-0.02	0.03	0.01	-0.06	-0.04
TZEI 378	-274.62	197.27	0.44	0.66	0.38	0.77	0.00	0.02	-0.01	0.08	0.04	-0.06	0.04	0.04
TZEI 379	-152.82	-171.49	-0.27	0.30	-0.34	0.29	-0.03	0.00	0.02	0.08	-0.07	0.11	0.00	-0.03
TZEI 402	-375.60	-130.65	0.37	-0.21	0.40	0.03	0.00	0.05	0.38*	-0.07	0.06	0.18	-0.04	-0.07
TZEI 449	456.77*	-262.45	0.81*	1.22*	0.64	1.41*	-0.04	0.04	-0.21	0.11	-0.11	0.22	0.08	-0.11*
TZEI 456	-12.46	-83.86	-0.52	-0.29	-0.56	-0.15	-0.03	0.03	0.06	0.12	-0.13	-0.07	-0.05	0.02
TZEI 461	-242.62	-450.92	0.51	-0.14	0.62	-0.11	0.04	0.04	0.11	0.05	0.17	0.14	0.18*	-0.06
TZEI 462	-97.32	-245.63	1.10*	0.92*	1.16*	0.78	0.02	-0.02	0.06	-0.11	0.28*	0.03	0.02	0.03
TZEI 467	-343.68	-142.79	-0.82*	-0.60	-0.85*	-0.67	0.00	-0.03	0.38*	0.22	0.33*	0.18	-0.04	-0.08
TZEI 468	-72.26	-145.08	-0.47	-0.75	-0.67	-0.83	-0.05	-0.02	0.20	0.32*	0.13	0.12	-0.05	-0.01
TZEI 470	-335.76	-186.17	0.64	-0.78	0.88*	-0.73	0.06	0.01	0.11	0.08	0.25*	0.17	-0.12*	-0.09
TZEI 472	16.72	-111.22	0.30	-0.09	0.34	-0.01	0.00	0.03	-0.12	0.03	-0.10	0.04	-0.01	-0.04
TZEI 475	-34.18	-212.82	-0.47	-0.02	-0.54	-0.09	-0.02	0.00	-0.16	-0.07	-0.08	-0.19	0.02	0.24**
TZEI 485	-139.47	-20.48	0.07	0.02	0.01	0.07	0.00	0.00	0.05	-0.17	-0.01	-0.17	-0.07	0.02
TZEI 497	-88.79	215.13	0.38	0.82*	0.20	0.78	-0.06	-0.01	-0.01	-0.18	-0.04	-0.26*	-0.05	-0.03
TZEI 520	-336.31	-293.13	1.15*	1.06*	1.44*	1.20*	0.05	0.03	0.18	0.10	0.07	0.15	-0.07	-0.01
SE	184.59	164.30	0.35	0.37	0.37	0.40	0.03	0.03	0.12	0.13	0.10	0.11	0.05	0.05

Table 5. 13

GCA, General combining ability, GCAm, GCA effects of the inbreds used as male parents, GCAf, GCA effects of the inbreds used as female parents, ASI, Anthesis-silking interval; *, ** Significant at probability levels of 0.05 and 0.01, respectively.

General combining ability effects of inbred lines for grain yield and other traits under *Striga* infestation

Inbred lines	Grain yield		Ear aspect		Ears per plant		*Striga* damage syndrome rating				Striga emergence count			
							8 weeks after plant		10 weeks after plant		8 weeks after plant		10 weeks after plant	
	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm
TZEI 3A	-17.65	-174.60	-0.08	0.20	-0.01	0.00	0.14	0.18	0.24	0.10	0.13	0.16	0.22	0.08
TZEI 8	46.82	164.98	-0.07	-0.32	0.03	0.12*	-0.16	-0.12	0	0.10	0.04	0.30*	0.06	0.20
TZdEI 40	175.23	219.43*	0.10	-0.62*	0.02	0.03	-0.12	-0.08	-0.05	-0.12	0.23	0.14	0.26	0.15
TZdEI 69	-103.88	-3.39	0.13	-0.17	-0.03	-0.04	-0.02	0.05	0.08	-0.24	0.41*	0.13	0.24	0.28
TZdEI 124	296.23*	128.49	-0.48*	0.07	0.06	0.06	0.02	-0.14	0.24	-0.07	0.42*	0.13	0.46*	0.18
TZEI 127	286.94*	219.29*	-0.32	-0.27	0.08*	-0.02	-0.36	-0.07	-0.39*	0.17	0.02	0.62*	-0.04	0.61*
TZdEI 192	-21.73	92.93	0.09	-0.16	0.01	0.06	-0.08	0.24	-0.34*	0.09	-0.22	-0.23	-0.38*	-0.30*
TZdEI 215	233.35	114.08	-0.11	-0.12	0.03	0.00	-0.31	0.09	-0.1	0.02	0.02	0.38*	0.06	0.28
TZdEI 216	129.74	203.86*	-0.11	-0.21	-0.02	0.01	-0.17	-0.57**	-0.40*	-0.36*	0.2	-0.34*	0.13	-0.12
TZdEI 238	80.88	-34.38	-0.30	-0.17	0.03	-0.01	-0.16	-0.11	-0.07	-0.18	0.16	0.04	0.15	0.03
TZdEI 272	-100.61	25.61	0.21	-0.34*	-0.03	0.01	-0.09	-0.08	-0.23	-0.17	0.13	-0.48*	-0.25	-0.57*
TZdEI 283	46.38	-73.02	-0.16	-0.07	0.01	0.05	0.22	-0.25	0.23	0.00	-0.17	0.32*	-0.14	0.18
TZEI 298	-186.45	-102.98	-0.04	0.23	-0.02	0.01	0.39*	0.20	0.15	0.10	-0.09	-0.31*	0.02	-0.16
TZEI 365	-136.73	-66.06	0.41*	0.16	-0.03	-0.05	-0.05	0.11	-0.02	0.27	-0.21	0.04	-0.12	-0.06
TZEI 376	-218.66	-121.00	0.28	0.09	-0.06	-0.06	0.27	-0.10	0.19	-0.12	-0.15	0.02	-0.1	0.14
TZEI 378	-183.79	30.10	0.41*	0.18	0.01	0.02	0.03	0.08	0.37*	0.01	-0.05	-0.32*	0.14	-0.41*

Table 5. 14

TZEI 379	111.53	-157.55	-0.27	0.28	0.04	-0.04	-0.06	0.69**	-0.29	0.59*	-0.38*	0.22	-0.37*	0.08
TZEI 402	71.35	137.87	0.02	0.04	0.03	-0.02	-0.13	-0.39**	-0.06	-0.05	-0.2	0.26	-0.04	0.36*
TZEI 449	76.22	-148.38	0.05	0.14	-0.02	-0.04	0.10	-0.34	0.03	-0.12	0.05	0.06	0.23	-0.05
TZEI 456	-100.00	-125.79	0.15	0.32	-0.02	0.06	0.18	0.02	0.28	-0.05	-0.13	0.04	0.09	-0.14
TZEI 461	145.07	42.95	-0.50*	-0.10	0.01	0.03	0.17	-0.10	0.19	0.11	0.52*	-0.37*	0.44*	-0.09
TZEI 462	58.56	-210.8*	-0.22	0.12	-0.01	-0.01	-0.14	0.40**	-0.19	0.26	0	-0.43*	0.18	-0.30*
TZEI 467	-154.03	65.18	0.21	-0.25	-0.04	-0.02	0.14	-0.14	0.12	-0.11	0.02	0.18	-0.08	0.11
TZEI 468	41.28	46.30	-0.03	0.02	-0.02	-0.01	-0.12	0.01	-0.07	0.08	-0.49*	-0.03	-0.39*	-0.01
TZEI 470	-43.84	203.35*	-0.05	-0.18	-0.02	-0.02	-0.10	-0.09	-0.25	-0.37*	0.03	-0.49*	-0.1	-0.40*
TZEI 472	-91.49	52.13	0.18	0.08	-0.01	-0.01	0.17	-0.22	0.18	-0.27	0.1	-0.41*	-0.15	-0.27
TZEI 475	-38.41	-88.04	-0.01	0.14	0.01	0.01	-0.20	0.37**	-0.01	0.16	-0.13	0.34*	-0.08	0.26
TZEI 485	-121.83	-157.28	0.18	0.18	0.09*	0.00	-0.16	0.00	-0.32	-0.05	-0.22	-0.03	-0.2	-0.21
TZEI 497	-40.77	-131.93	0.08	0.21	0.00	-0.06	0.37	0.18	0.22	0.23	0.01	-0.21	-0.11	-0.01
TZEI 520	-239.77	-151.41	0.26	0.52*	-0.11*	-0.05	0.23	0.17	0.25	-0.02	-0.03	0.28	-0.11	0.15
SE	110.28	86.74	0.18	0.15	0.03	0.03	0.17	0.16	0.16	0.15	0.17	0.14	0.12	0.13

GCA, General combining ability, GCAm, GCA effects of inbreds used as male parents, GCAf, GCA effects of the inbreds used as female parents, *, **, Significant at probability levels of 0.05 and 0.01, respectively

General combining ability effects of inbred lines for grain yield and other traits under low-N environments

Inbred line	Grain yield		Days to anthesis		Days to silking		Plant aspect		Ears aspect		Ears per plant		Stay green	
	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm
TZEI 3A	-207.61	-152.47	-0.86	-0.47	-0.98	-0.31	0.19	0.02	-0.01	-0.06	-0.06	-0.10	0.05	0.04
TZEI 8	70.41	281.25	-1.13	-0.91	-1.03	-1.21	-0.07	0.02	0.26	0.00	0.09	0.02	-0.26*	0.38*

Table 5. 15

TZdEI 40	305.8	-113.01	-0.22	-0.15	-0.17	0.53	-0.12	0.04	-0.20	0.13	0.03	-0.04	0.08	0.31*
TZdEI 69	69.49	59.31	-0.17	-0.74	-0.22	-0.65	0.00	0.23	-0.18	0.11	-0.02	-0.11	-0.25*	0.25
TZdEI 124	115.43	398.78*	-1.14	-0.86	-1.01	-1.16	-0.15	0.06	0.10	-0.06	0.04	0.05	0.38**	0.1
TZEI 127	179.44	359.03	0.00	-1.26	0.37	-0.96	-0.20	0.01	0.06	-0.03	0.04	0.06	-0.25*	-0.31*
TZdEI 192	544.78*	-103.67	-0.54	0.25	-0.81	0.38	-0.08	-0.21	-0.07	-0.02	0.01	0.03	-0.24*	-0.44*
TZdEI 215	468.93	425.60*	-0.22	1.14	-0.10	1.14	-0.08	0.03	0.10	0.05	-0.03	-0.12*	-0.50**	0.11
TZdEI 216	-3.93	226.17	-0.59	-0.56	-0.79	-0.66	-0.05	-0.27	0.06	-0.01	0.03	0.00	0.36**	0.04
TZdEI 238	-337.36	-99.71	0.52	0.71	0.73	1.37	0.13	0.20	0.10	0.09	-0.09	0.03	0.12	0.18
TZdEI 272	448.6	306.44	-0.84	-0.47	-0.96	0.32	-0.11	-0.21	-0.25	0.02	0.08	0.11	-0.52**	-0.82*
TZdEI 283	38.79	-310.54	0.25	0.24	0.44	0.11	0.07	0.10	0.07	0.00	-0.04	0.02	-0.08	-0.47*
TZEI 298	-625.96*	-391.05*	1.13	0.37	1.03	0.05	0.02	0.10	0.10	-0.03	0.01	0.13*	0.39**	0.25*
TZEI 365	-296.3	2.58	0.67	-0.28	0.49	-0.67	0.18	-0.09	0.03	-0.01	0.07	-0.03	-0.30*	0.06
TZEI 376	-26.54	-197.98	0.49	0.18	0.59	0.07	-0.08	0.03	-0.16	0.00	-0.03	-0.08	0.04	0.11
TZEI 378	-256.47	66.71	0.94	1.11	1.20	1.51	-0.01	-0.06	0.09	0.00	0.07	0.04	0.14	0.19
TZEI 379	152.13	-41.67	-0.43	-0.06	-0.64	-0.32	-0.01	0.00	-0.04	-0.09	-0.04	0.04	-0.18	-0.02
TZEI 402	-83.98	-188.51	0.79	-0.58	1.00	-1.2	-0.01	0.06	0.06	0.03	0.01	-0.02	0.59*	0.42*
TZEI 449	593.89*	55.12	-0.22	0.68	-0.14	0.81	-0.21	0.17	-0.24	0.01	0.05	-0.04	-0.22*	-0.09
TZEI 456	-52.06	-2.46	-0.59	-0.71	-0.46	-1.11	0.08	-0.19	-0.02	-0.05	-0.05	0.07	0.34**	0.21
TZEI 461	-317.45	-230.16	-0.35	0.32	-0.65	-0.43	0.07	0.02	0.15	-0.06	-0.07	0.06	0.26*	-0.26*
TZEI 462	53.05	-209.46	0.31	1.28	0.02	1.33	-0.05	0.05	-0.09	0.00	0.08	-0.05	-0.45**	0.11
TZEI 467	-43.93	196.02	-0.39	-0.76	-0.12	-0.95	0.06	-0.05	0.01	-0.08	0.02	0.02	0.09	0.19
TZEI 468	-43.37	3.62	-1.78*	-0.36	-1.99	-0.55	0.03	0.07	0.09	0.00	0.07	-0.07	-0.02	0.17
TZEI 470	-652.82*	-101.1	1.79*	-0.91	2.31*	-0.84	0.17	-0.07	0.04	0.17	-0.16*	0.06	0.19	-0.44*
TZEI 472	-136.49	-343.13	0.66	1.45	0.19	1.69	0.11	0.17	0.05	0.17	-0.08	-0.11	0.27*	-0.2
TZEI 475	-59.53	-363.21	-1.53	-0.32	-1.80	-0.37	-0.03	-0.15	-0.16	-0.09	0.04	0.01	-0.09	-0.14
TZEI 485	146.84	143.26	0.29	-0.03	0.59	0.27	-0.14	0.06	-0.05	0.08	0.02	0.03	-0.44**	-0.37*
TZEI 497	48.06	127.94	1.09	1.46	0.66	1.62	0.15	0.02	0.11	-0.10	-0.02	-0.05	0.38	0.29*
TZEI 520	-91.82	196.29	2.06*	0.21	2.22*	0.19	0.16	-0.19	0.01	-0.15	-0.04	0.01	0.12	0.16
SE	188.59	131.04	0.61	0.55	0.75	0.77	0.09	0.12	0.10	0.08	0.05	0.04	0.07	0.09

GCA, General combining ability, GCAm, GCA effects of the inbreds used as male parents, GCAf, GCA effects of the inbreds used as female parents, *, **, Significant at probability levels of 0.05 and 0.01, respectively

General combining ability effects of inbred lines for grain yield and agronomic traits evaluated across optimal

Table 5. 16
low soil nitrogen and artificial *Striga*-infested environments

	Grain yield		Days to anthesis		Days to silking		Plant aspect		Ear aspect		Ears per plant	
Inbred line	**GCAf**	**GCAm**	**GCAf**	**GCAm**	**GCAf**	**GCAm**	**GCAf**	**GCAm**	**GCAf**	**GCAm**	**GCAf**	**GCAm**
TZEI 3A	-179.48	-99.70	-0.25	-0.05	-0.45	-0.18	0.08	-0.10	0.02	0.03	-0.04	-0.04
TZEI 8	30.82	305.62*	-1.08**	-0.93**	-0.81*	-1.10**	0.11	-0.03	0.04	-0.02	0.06*	0.05*
TZdEI 40	466.98**	459.70**	-0.79*	-0.18	-0.97*	-0.41	-0.26*	-0.22*	-0.19*	-0.31**	0.01	0.04
TZdEI 69	104.57	13.44	-0.48*	-1.09**	-0.51	-0.93*	0.14	0.13	-0.04	-0.02	-0.01	-0.05*
TZdEI 124	308.02*	257.75*	-1.15**	-0.94**	-1.05*	-1.13**	-0.15	0.02	-0.18*	-0.14	0.03	0.05
TZEI 127	339.24*	390.15**	0.06	-0.37	-0.26	-0.33	-0.37**	-0.27*	-0.30*	-0.16*	0.08*	0.04
TZdEI 192	272.6*	-76.59	0.35	0.27	0.14	0.11	0.04	-0.14	0.03	-0.01	0.09*	0.03
TZdEI 215	417.62**	231.12*	-0.66*	0.47*	-0.27	0.63*	-0.14	-0.03	-0.06	-0.05	0.00	0.00
TZdEI 216	33.00	189.71*	-0.11	-0.35	-0.11	-0.33	-0.11	-0.14	0.03	-0.05	-0.01	0.00
TZdEI 238	-122.46	-39.18	0.01	-0.26	0.28	-0.06	0.09	-0.06	-0.07	-0.05	-0.05	0.00
TZdEI 272	260.29*	108.40	-0.22	0.17	-0.25	0.09	0.06	-0.05	-0.15	-0.18*	0.06*	0.09*
TZdEI 283	83.16	-191.57*	0.32	0.56*	0.35	0.38	0.03	-0.08	-0.04	-0.03	-0.02	0.03
TZEI 298	-351.91*	-205.01*	0.61*	0.23	0.58*	-0.16	-0.05	0.21*	0.12	0.12	-0.02	-0.01
TZEI 365	-249.36*	-151.07	0.44	0.52*	0.20	0.66*	-0.01	0.21*	0.12	0.17*	-0.02	-0.02
TZEI 376	-208.8*	9.06	0.34	0.41	0.43	0.42	0.03	-0.04	0.09	0.04	-0.05	-0.06*
TZEI 378	-234.66*	96.27	0.33	0.66*	0.54*	0.65*	0.07	0.14	0.20*	0.08	0.03	0.03
TZEI 379	13.91	-107.85	-0.06	0.22	-0.27	0.23	-0.12	-0.06	-0.14	0.02	0.01	-0.01
TZEI 402	-146.52	-34.81	0.52*	-0.83*	0.39	-0.38	0.05	-0.03	0.07	0.09	0.00	-0.04
TZEI 449	353.90*	-172.75*	0.71*	1.13**	0.55*	1.13**	-0.17	0.27*	-0.14	0.09	0.03	-0.08*
TZEI 456	-23.89	-43.99	-0.96**	-0.41	-0.79*	-0.55*	0.05	0.14	-0.09	-0.04	-0.03	0.05
TZEI 461	-169.83	-216.79*	-0.14	-0.51*	0.06	-0.28	0.22*	0.17	0.02	-0.02	0.05	0.00
TZEI 462	-9.87	-227.23*	0.62*	1.02**	0.87*	1.14**	0.01	0.07	0.10	0.08	0.03	0.00
TZEI 467	-245.12	5.39	-0.10	-0.56*	-0.01	-0.51	0.29*	0.11	0.30*	-0.03	-0.04	-0.04
TZEI 468	23.80	-67.34	-0.69*	-0.58*	-0.59*	-0.73*	-0.01	0.17	0.02	0.07	-0.01	-0.04
TZEI 470	-314.45*	-7.70	0.91**	-0.56*	0.86*	-0.53	0.12	-0.14	0.16	0.02	-0.09*	-0.03
TZEI 472	-60.35	-124.31	0.38	0.31	0.20	0.25	0.02	-0.06	-0.01	0.15	-0.03	-0.04
TZEI 475	-25.28	-229.47*	-0.85**	-0.17	-0.81*	-0.01	-0.14	-0.04	-0.11	-0.01	0.03	0.09*
TZEI 485	-67.18	-11.75	0.38	0.26	0.26	0.41	-0.12	-0.09	0.07	0.03	0.01	0.03
TZEI 497	-44.98	104.32	0.31	0.52*	0.21	0.51	0.08	-0.05	0.06	-0.07	-0.02	-0.04
TZEI 520	-253.75*	-163.81	1.25**	1.01**	1.24**	1.01*	0.16	-0.03	0.09	0.23*	-0.06*	-0.03
SE	93.38	81.87	0.23	0.23	0.27	0.27	0.10	0.09	0.08	0.08	0.03	0.02

GCA, General combining ability, GCAm, GCA effects of the inbred useds as male parents, GCAf, GCA effects of the inbreds used as female parents, *, **, Significant at probability levels of 0.05 and 0.01, respectively

Table 5. 17

5.3.4 Heterotic groupings of inbred lines, and relationships among heterotic grouping methods

The summary of the groupings of the 30 inbred lines using dendrograms based on HGCAMT, and SSRand SNP genetic distance (GD) methods are presented in Table 5.16 and in Appendices 5 to 10. The HGCAMT grouping method identified three groups each under low-N, optimal growing conditions and across research environments and four groups under *Striga*-infested environments. In contrast, the SSR-GD and SNP-GD methods clustered the inbred lines into seven and five groups, respectively. However, the SSR-GD method could not classify the inbred lines TZEI 468, TZdEI 40 and TZEI 127 into any heterotic group. The classification of the inbreds into heterotic groups by all three methods was based on pedigree and selection history with similar trends as described in Chapter 3, Section 3.5. Generally, there was very little correspondence between the three grouping methods in terms of placement of inbred lines into the same heterotic group (Table 5.16).

Table 5. 16 Summary of the heterotic groups of 30 early maturing maize inbred lines identified by the general combining ability of multiple traits (HGCAMT), Single Sequence Repeat (SSR) and Single Nucleotide Polymorphism (SNP) based Genetic Distance (GD) methods under each and across contrasting environments

Method	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
HGCAMT-*Striga*	TZEI 3A, TZdEI 283, TZEI 456, TZdEI 69, TZEI 378, TZEI 467, TZEI 298, TZEI 497, TZEI 365, TZEI 376, TZEI 520	TZdEI 192, TZEI 468, TZdEI 272, TZEI 470, TZEI 472	TZEI 379, TZEI 449, TZEI 462, TZEI 485	TZEI 8, TZdEI 40, TZdEI 216, TZEI 127, TZdEI 215, TZdEI 238, TZEI 402, TZEI 475, TZdEI 124, TZEI 461			
HGCAMT-Low-N	TZEI 3A, TZEI 468, TZdEI 69, TZEI 8, TZdEI 124,TZEI 402, TZEI 456, TZEI 467	TZdEI 238, TZEI 472, TZdEI 283, TZEI 461, TZEI 470,TZEI 298, TZEI 365, TZEI 378, TZEI 497, TZEI 520	TZdEI 40, TZdEI 215, TZEI 127, TZdEI 216, TZdEI 192, TZEI 379, TZEI 485, TZEI 449, TZEI 475,TZEI 376,TZEI 462, TZdEI 272				
HGCAMT-Optimal	TZEI 3A, TZdEI 283,TZEI 485,TZEI 497, TZdEI 216, TZdEI 238,TZEI 192, TZdEI 272, TZEI 475,TZEI 8,TZdEI 69, TZdEI 124	TZEI 298, TZEI 376, TZEI 378, TZEI 365, TZEI 379, TZEI 472, TZEI 456,TZEI 449, TZEI 462, TZEI 520,TZEI 461, TZEI 402 TZEI 470, TZEI 467, TZEI 468	TZdEI 40, TZEI 127, TZdEI 215				

Table 5.16 Cont'd

Method	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
HGCAMT-Across	TZEI 3A, TZEI 376, TZEI 472, TZEI 520, TZEI 462, TZEI 485, TZEI 497, TZEI 449, TZEI 298, TZEI 365, TZEI 378, TZEdEI 69, TZEI 468, TZEI 402, TZEI 470, TZEI 467	TZdEI 192, TZdEI 272, TZdEI 238, TZdEI 283, TZEI 379, TZEI 456, TZEI 475, TZEI 461	TZEI 8, TZdEI 124, TZdEI 40,TZEI 127, TZdEI 215,TZdEI 216				
SSR-GD	TZdEI 283, TZEI 298, TZdEI 272, TZdEI 124, TZEI 365, TZEI 376, TZEI 378, TZEI 379, TZdEI 238	TZEI 472, TZEI 470, TZEI 467	TZEI 8, TZEI 497, TZEI 3A, TZdEI 192, TZEI 402, TZdEI 215, TZdEI 216, TZdEI 69, TZEI 461, TZEI 520, TZEI 485, TZEI 456, TZEI 449	TZEI 462, TZEI 475	TZdEI 40	TZEI 127	TZEI 468
SNP-GD	TZEI 8, TZEI 127, TZdEI 40, TZEI 192, TZdEI 283, TZdEI 216, TZdEI 69, TZdEI 124, TZdEI 272,	TZdEI 215, TZdEI 238	TZEI 365, TZEI 376, TZEI 298, TZEI 378, TZEI 379, TZEI 3A, TZEI 402	TZEI 468, TZEI 467, TZEI 472, TZEI 470	TZEI 461, TZEI 462, TZEI 497, TZEI 475, TZEI 449, TZEI 485, TZEI 520, TZEI 456		

5.3.5 Comparison of different methods of heterotic grouping for early maturing maize inbred lines under contrasting environments

Out of the 150 hybrids tested, the HGCAMT method classified 36, 36, 34 and 37 of them as higher yielding and 30, 18, 19 and 29 of them as low yielding under optimal, *Striga* infestation, low-N, and across environments, respectively (Table 5.17); the SSR-GD method classified 30, 31, 27 and 30 of the hybrids as high yielding and 21, 21, 20 and 20 of the hybrids as low yielding under optimal, *Striga* infested , low-N, and across environments, respectively. However, the SNP-GD method identified 36, 41, 38, and 43 of the hybrids as high-yielding and 22, 25, 27 and 21 of them as low-yielding hybrids under optimal, *Striga* infested, low-N, and across environments, respectively (Table 5.17). The breeding efficiency of the SNP-GD method was the highest under *Striga* (44%), low-N (45%) and across environments (50.81%), while the breeding efficiency of HGCAMT method was the highest under optimal growing conditions (Table 5.17). The breeding efficiencies of HGCAMT and SSR-GD methods were comparable under *Striga* infestation (Table 5.17).

Table 5. 17 Number of inter- and intra-group hybrids classified by the HGCAMT,

SSR, and SNP genetic distance based methods, along with the breeding efficiency (BE) of the methods under optimal, *Striga*-infested, low-N and across environments

Yield Group	Cross type	Optimal		
		HGCAMT	**SSR-GD**	**SNP-GD**
1	inter-group	36	30	36
1	intra-group	14	20	14
2	inter-group	31	36	30
2	intra-group	19	14	20
3	inter-group	20	29	28
3	intra-group	30	21	22
BE		**44.50**	**34.88**	**38.79**
Yield Group	**Cross type**	***Striga*-infested**		
		HGCAMT	**SSR-GD**	**SNP-GD**
1	inter-group	36	31	41
1	intra-group	14	19	9
2	inter-group	38	36	28
2	intra-group	12	14	22
3	inter-group	32	29	25
3	intra-group	18	21	25
BE		**37.44**	**35.59**	**44.13**
Yield Group	**Cross type**	**Low-N**		
		HGCAMT	**SSR-GD**	**SNP-Based**
1	inter-group	34	27	38
1	intra-group	16	23	12
2	inter-group	36	38	35
2	intra-group	14	12	15
3	inter-group	31	30	23
3	intra-group	19	20	27
BE		**36.22**	**32.39**	**44.79**
Yield Group	**Cross type**	**Across environments**		
		HGCAMT	**SSR-Based**	**SNP-Based**
1	inter-group	37	30	43
1	intra-group	13	20	7
2	inter-group	31	34	33
2	intra-group	19	16	17
3	inter-group	21	30	19
3	intra-group	29	20	31
BE		**44.56**	**33.81**	**50.81**

5.4 Discussion

The presence of broad genetic diversity among breeding lines is the most useful indicator of expected gains from selection (Falconer, 1989). The significant differences detected among the hybrids for grain yield and most of the traits measured under each and across the three contrasting environments indicated that there was adequate genetic variability among the hybrids to allow good progress from selection for improvements of desired traits under optimal, low-N and *Striga*-infested environments. This result is consistent with the findings of Badu-Apraku *et al.* (2011b) and Badu-Apraku and Oyekunle (2012). The significant differences observed among environments indicated that the test environments were diverse and therefore could effectively reveal the differences among the hybrids. The significant GEI detected for grain yield and the other traits under optimal, *Striga*-infested and low-N environments and across environments indicated that the expression of these traits would vary in the contrasting environments. This result justified the need for extensive testing of genotypes in multiple environments, including locations and years before genotype recommendations are made (Badu-Apraku *et al.*, 2017).

The significant GCAm, GCAf and SCA for grain yield and the other traits under optimal, *Striga*-infested and low-N environments and across environments indicated that there were significant differences in the performance of the inbred lines as parents in hybrid combination for those traits. These results also suggested that both additive and nonadditive gene actions were important for the inheritance of grain yield and the other traits under each environment and across the three research environments. This result is

consistent with the findings of Badu-Apraku *et al.* **(**2015). However, it is inconsistent with the findings of Ifie *et al.* (2015) who reported non-significant SCA effects for number of emerged *Striga* plants under *Striga*-infested environments and for the stay green characteristic under low-N environments. The lack of significance of GCAm, GCAf and SCA for anthesis-silking interval under each and across the three research environments indicated that the inheritance of anthesis-silking interval in the tested hybrids is not controlled by either additive or non-additive gene actions but by other modes of inheritance. The significant GCAm x E and GCAf x E interactions for grain yield and most of the other traits measured under optimal, low-N and *Striga*-infested and across environments indicated that the GCA effects of the inbred lines varied in the different environments. This result is consistent with the findings of Annor and Badu-Apraku (2015) for grain yield and other traits of extra-early QPM inbred lines under optimal and low-N environments and across both environments. The non-significant GCAm x E interaction for grain yield under low-N and *Striga*-infested environments indicated that the GCA effects associated with the inbred lines for grain yield were consistent over low-N and *Striga*-infested environments when the inbred lines were used as male parent, and that it may not be necessary to carry out selection for improvement in grain yield in specific environments. The non-significant SCA x E interaction for grain yield, plant height and stay green characteristic under low-N environments indicated that the expression of the traits in specific hybrid combinations would be stable under low-N environments. Similarly, the non-significant SCA x E interaction for anthesis-silking interval, ear height, husk cover, *Striga* damage syndrome rating at 8 WAP, and for number of emerged *Striga* plants at 8 and 10 WAP under *Striga*-infested environments indicated that the expression

of these traits in specific hybrid combinations would be stable under *Striga*-infested environments. These results are consistent with the findings of Ifie *et al.* (2015) who reported non-significant SCA x E interactions for grain and stay green characteristic under low-N; for *Striga* damage syndrome rating at 8 WAP, number of emerged *Striga* plants at 8 and 10 WAP under *Striga*-infested environments.

The larger GCA variance obtained over that of SCA in the present study for days to silking, days to anthesis, ear height and plant height under optimal growing conditions indicated that additive gene action largely modulated the inheritance of those traits under optimal growing conditions. Musila *et al.* (2010) also found additive gene action to be more important than non-additive gene action in the inheritance of days to anthesis for early maturing inbred lines in optimal environments. The larger GCA sum of squares obtained over SCA sum of squares for grain yield, plant height and stalk lodging under low-N environments, and for grain yield, days to anthesis and silking, plant height and ear height across environments, indicated that additive gene action largely controlled the inheritance of those traits under the respective test environments. The importance of additive gene action over non-additive gene effects in the inheritance of grain yield under low-N as observed in this study is in agreement with the results of Rizzi *et al.* (1993); Below *et al.* (1997) and Kling *et al.* (1997). However, the present results disagreed with the findings of Betra´n *et al.* (2003b) who found non-additive gene action to be more important in the inheritance of grain yield under low-N. Also, the predominance of GCA over SCA sum of squares for days to silking, days to anthesis, ear height and plant height under optimal growing conditions, and for grain yield, plant height and stalk lodging under low-N environments and for grain yield, days to anthesis, days to silking, plant height and ear

height across environments. This result implied that early generation testing may be more effective for those traits and that promising hybrids can be identified and selected mainly based on the prediction from GCA effects (Baker, 1978; Badu-Apraku *et al*., 2015). However, since SCA effects of the inbred lines were also significant, prediction of hybrid performance based solely on GCA effects of the parents might not be reliable. Furthermore, the preponderance of additive gene action indicated the existence of a great potential for the improvement of those traits under optimal and low-N environments through recurrent selection methods (Badu- Apraku *et al.*, 2011b).

The preponderance of SCA sum of squares over GCA sum of squares for grain yield and almost all other measured traits under *Striga* infestation revealed the importance of nonadditive genetic effects over additive genetic effects in the inheritance of *Striga* resistance and/or tolerance. This result agrees with the findings of Badu-Apraku *et al.* (2015) who reported larger proportion of SCA sum of squares over GCA sum of square for grain yield and almost all other traits measured under *Striga* infestation except for days to anthesis and ears per plant. Kim (1994) also found larger SCA sum of squares over GCA sum of squares for number of emerged *Striga* plants at 8 and 10 WAP. However, this result contradicted the results of Gethi and Smith (2004), Yallou *et al.* (2009), Badu-Apraku and Oyekunle

(2012) and Ifie *et al.* (2015) who reported larger proportion of GCA sum of squares over SCA sum of squares for *Striga* damage syndrome rating at 8 WAP and number of emerged *Striga* plants at 8 and 10 WAP in early maturing maize inbreds. Under low-N environments, the inheritance of plant aspect, ear aspect, ears per plant, stay green characteristic, days to silking and anthesis–silking interval were also controlled by

nonadditive gene action. Across the three research environments, the inheritance of stalk lodging, husk cover, plant aspect, ear aspect and ears per plant were also controlled by nonadditive gene action. Unlike the traits controlled by additive gene action, non-additive genetic effect is rarely predicted because a prediction of such gene combinations has little practical use, since they are not transmitted from parents to offspring (Beckett and Ludwick, 1979; Hu *et al.* (2011). Therefore, hybrid development could be employed to exploit non-additive genetic effects such as heterosis to improve grain yield and the other traits under *Striga*-infestation and low-N environments (Menkir and Akintunde (2001).

The larger sum of squares of GCAf compared to the sum of squares of GCAm observed for grain yield and almost all the other measured traits under optimal, *Striga*-infested and low-N environments and across environments, indicated that maternal inheritance played an important role in the inheritance of grain yield and the other traits under each of the three research environments and across environments. This result implied a possible role of cytoplasmic gene effects on grain yield and its components under all the research environments. These results corroborated the findings of Derera *et al.* (2008) who reported that maternal effects modified grain yield under drought/low-N as well as anthesis-silking interval and ear aspect under well-watered environments in maize hybrids. Similarly, Oyekunle and Badu-Apraku (2014) found that the inheritance of grain yield under optimal conditions is controlled by maternal effects. On the contrary, the larger GCAm effects observed over GCAf effects for anthesis–silking interval, plant aspect, husk cover and ears per plant under low-N, and for number of emerged *Striga* plants at 8 and 10 WAP, days to silking, ears per plant and days to anthesis indicated that the traits were controlled by paternal effects. Under low-N, the observed similarities in the magnitude of contributions

of GCAf and GCAm for root and stalk lodgings and stay green characteristic, indicated that both maternal and paternal effects played similar roles in the inheritance of those traits under low-N environments. The maternal and paternal effects on the inheritance of anthesis–silking interval, plant height and husk cover under optimal conditions were also similar. Similarly, the role played by maternal effects in the inheritance of plant height, husk cover and ear aspect under *Striga* infestation as well as the inheritance of days to anthesis, root lodging, husk cover and plant aspect across the three research environments were similar to the role played by paternal effects. These results contradicted the findings of Ifie (2013) that indicated no cases of maternal or paternal effects on traits under low-N and optimal environments. Generally, the differences in the mode of inheritance of traits as observed in the set of early maturing inbred lines tested in the present study when compared to results of earlier workers may be attributed to the differences in the germplasm used.

Combining ability of an inbred line is the ultimate factor determining its future usefulness and commercial potential in hybrid development (Hallauer and Miranda, 1988). Information on GCA genetic effects of breeding lines is a crucial guide for the selection of parents and planning of crosses that would attain the optimal expression of desired traits under target environments. Inbred lines displaying significant and positive GCA effects for traits such as grain yield and ears per plant (traits measured such that higher values are desirable) indicates a potent evidence of desirable gene flow from parents to progenies at high intensity, and the opposite holds for inbred lines that showed significant and negative GCA effects. For traits measured such that lower values are desirable, like days to anthesis, days to silking, anthesis-silking interval, plant aspect, ear aspect, *Striga* damage syndrome

rating and number of emerged *Striga* plants and the stay green characteristic, significant negative GCA effects are rather desirable. The significant positive GCAf effects obtained by TZdEI 40, TZdEI 124, TZEI 127, TZdEI 192, TZdEI 215 and TZEI 449 for grain yield, and the significant positive GCAm effects for grain yield exhibited by TZEI 8, TZdEI 40 and TZEI 127 under optimal growing conditions suggested that the inbred lines could contribute favourable genes to improve grain yield in their progenies when used as female and male parents, respectively. The significant negative GCAm and GCAf effects obtained by TZEI 8, TZdEI 69, TZdEI 124 for days to anthesis, and by TZEI 8 and TZdEI 124 for days to silking indicated that the inbred lines could contribute favourable genes to improve those traits in their progenies when used either as male or female parent under optimal growing conditions. Under *Striga* infestation, TZdEI 124 and TZEI 127, and TZdEI 40, TZEI 127, TZdEI 216, TZEI 470 would contribute favorable genes to improve the yielding potential of their progenies when used as female and male parents, respectively. The inbred lines TZEI 127, TZdEI 192, TZdEI 216, TZEI 298 and TZEI 402 were superior with significant negative effects for both GCA_m and GCA_f for *Striga* damage syndrome ratings and number of emerged *Striga* plants at 8 and 10 WAP. According to Badu-Apraku *et al.* (2015), when searching for traits to be used as indirect selection criteria for grain yield, an ideal trait must have similar or neutral GCA effects as grain yield. However, for traits where decrease in a secondary trait leads to increase in the primary trait such as anthesissilking interval, plant aspect, or ear aspect versus grain yield, contrasting GCA effects are desirable in the two traits. Therefore, TZEI 127, TZdEI 216 and TZEI 470 will be very desirable in recurrent selection program and could be used as parents to develop synthetic populations that could be improved for *Striga* resistance and improved grain

yield. Furthermore, they could be used to develop outstanding *Striga* resistant hybrids for commercialization in *Striga* endemic areas of SSA.

It is important to note that, the lack of significant GCA effects of the 30 inbred lines for almost all traits measured in low-N environments, except for grain yield and stay green characteristic should be of great concern, where breeding efforts are geared towards multiple trait selection and improvement. The significant and positive GCAm and GCAf effects for grain yield obtained by TZdEI 192 suggested that the inbred line could contribute favourable genes to improve grain yield in its progeny when used either as male or female parent. The negative and significant GCAm and GCAf effects of stay green characteristic for TZdEI 192, TZEI 127, TZdEI 272, and TZEI 485 suggested that they would contribute alleles that would delay leaf senescence in their progenies when used either as male or female parents. On the contrary, the negative and significant GCAf effects exhibited by TZdEI 69, TZEI 8 and TZEI 365 indicated that these inbred lines would contribute alleles to delay leaf senescence in their progeny when used only as a female parent. Therefore, inbred lines TZdEI 192, TZEI 127, TZdEI 272, TZEI 485, TZdEI 69, TZEI 8 and TZEI 365 would be ideal choice for recurrent selection methods/programs aimed at improving stay green characteristic, while TZdEI 192 can also be used as a male parent to develop hybrids with improved yield and low-N tolerance.

The following inbred lines had superior GCA effects when used as either male or female parent across contrasting environments: TZdEI 40 for grain yield, days to anthesis, plant aspect and ear aspect; TZdEI 124 for grain yield, days to silking and anthesis; TZEI 127 for grain yield, plant and ear aspects, and TZdEI 215 for grain yield and days to anthesis. They are therefore ideal parents for the development of hybrids with multiple stress

resistance to *Striga* infestation and low-N environments and could be used for improvement of tropical breeding populations.

A heterotic group is a collection of closely related genotypes in a way that genetically divergent groups are assigned to different groups. Ideally, a cross of inbred lines from different heterotic groups should result in vigorous and productive hybrids, but not when inbred lines from the same heterotic group are crossed (Lee, 1995). Information on heterotic patterns of germplasm in every hybrid development program is important as genetically divergent parents are required to attain the highest expression of heterosis. The HGCAMT heterotic grouping method clustered the 30 inbred lines used in the present study into three genetically distinct groups each under low-N, optimal growing conditions and across research environments and four groups under *Striga*-infested environments. On the other, the SSR-GD and SNP-GD methods identified seven and five genetically distinct groups, respectively. The differences in the number of clusters formed by the three methods, coupled with the little correspondence between the methods in terms of placement of the inbred lines into the same heterotic group, showed that some of the methods were more efficient in grouping the inbred lines than others.

According to Fan *et al*. (2009) and Badu-Apraku *et al.* (2015), the breeding efficiency of a heterotic grouping method is the percentage of high-yielding hybrids across the total number of inter-heterotic crosses, implying that the best heterotic grouping method is the one that allows more inter-heterotic group crosses to produce more superior hybrids than the intragroup crosses. Therefore, the highest breeding efficiency obtained for the SNPGD over the HGCAMT and SSR-GD methods for the groupings of the inbred lines under

Striga-infested, low-N environments and across environments, indicated that the SNP-GD method was the most efficient heterotic grouping method in the present study; followed by the HGCAMT, while the SSR-GD was the least efficient in grouping the inbred lines under each and across the three research environments. This result is consistent with the findings of Badu-Apraku *et al*. (2015a, b) that indicated superiority of the SNP-GD method over HGCAMT method in groupings of early maturing inbred lines. This result is also in agreement with the results of Badu-Apraku *et al*. (2013) that indicated superiority of the HGCAMT method over SSR-GD methods in the heterotic groupings of early maturing inbred lines. Moreover, the superior performance of the SNP-GD method over the HGCAMT method also suggests that SNP markers can be used to group inbred lines in the IITA maize program that are yet to be field tested in hybrid combinations. This result is consistent with reports by Badu-Apraku *et al. (*2013a) and Akinwale *et al*. (2014). Since the SNP-GD was identified as the most efficient in grouping the inbred lines, it would be more suitable to rely on the grouping by the SNP-GD method to select parent lines from the tested inbred lines for the development of high-yielding hybrids and synthetic varieties. Crosses should be planned between opposite heterotic groups for the development of productive hybrids with tolerance to either *Striga* infestation or low-N or both stresses. Furthermore, inbred lines within clusters could be recombined to form heterotic populations that could be improved through recurrent selection for *Striga* resistance and low-N tolerance to serve as germplasm sources for tropical maize breeding programs.

CHAPTER SIX

6.0 Estimation of heterosis for grain yield and its component traits in early maturing hybrids under optimal growing conditions, *Striga*-infested and low-N environments

6.1 Introduction

Heterosis is the hybrid vigour manifested in hybrids. It represents the superiority or inferiority in performance of hybrid individuals compared with their parents (Mulualem and Abate, 2016). The phenomenon of heterosis has provided the most important genetic tool to improve yield potential of crop plants. It has had its most significant expression in maize, being intensively explored by breeders and seed production companies (Paterniani, 2001). The degree of expression of heterosis depends on the gene action controlling the trait of interest and genetic divergence of parents. It is manifested in the offspring of inbred lines with high specific combining ability (Mulualem and Abate, 2016). Heterosis in maize appears to increase with increased genetic divergence of the parent populations over a rather wide range of diversity (Moll *et al.*, 1962).

Heterosis helps to identify parents and their cross combinations capable of producing the highest level of transgressive segregates. The present study was carried out to determine the direction and magnitude of heterosis of the 150 early maturing single-cross hybrids of North Carolina design II crosses involving 30 inbred parents under low-N, *Striga*-infested and optimal environments and across environments.

6.2 Materials and methods

6.2.1 Genetic materials

The 150 single-cross hybrids used in Chapter 5 Section 5.2.1 were used in this study.

6.2.2 Field procedures

The hybrids were evaluated under optimal growing conditions, low-N and *Striga*-infested environments as described in Chapter 5 Section 5.2.2.

6.2.3 Data collection

The data used in this study were the same as described in Chapter 5, Section 5.2.2.

6.2.4 Statistical analysis

Estimates of heterosis over mid-parent and better-parent (BPH) were computed according to the procedures outlined by Hallauer and Miranda (1988) as

$$Mid - parent\ heterosis(MPH) = \left(\frac{F_1 - MP}{MP}\right) x100$$

$$Better - parent\ heterosis(BPH) = \left(\frac{F_1 - BP}{BP}\right) x100$$

Where F_1 is the mean of the F_1 cross, MP is the mid-parent value of a particular F_1 cross [(P1 + P2)/2], BP is the better parent value of a F_1 cross (P_1 or P_2), P_1 and P_2 are the parents of the hybrid. The test of significant difference for MPH and BPH was estimated using ordinary t-test according to the relationship described by Paschal and Wilcox (1975):

$$t - test\ for\ Mid - parent\ heterosis\ (MPH) = \frac{(F_1 - MP)}{\sqrt{\frac{3}{2r}(EMS)}}$$

$$t - test\ for\ Better - parent\ heterosis\ (BPH) = \frac{(F_1 - BP)}{\sqrt{\frac{2}{r}(EMS)}}$$

Where r is the replication, *EMS* is Error Mean square.

The *t* calculated values were compared with *t*-tabulated value for error degree of freedom at 5 % significance level (Hallauer & Miranda, 1988).

6.3 Results

6.3.1 Heterosis for grain yield and its component traits in early maturing hybrids under optimal growing conditions

The estimates of mid-parent and better-parent heterosis for days to silking were significant under optimal growing conditions. Mid-parent heterosis for days to anthesis was also significant (Appendix 11). The hybrid TZdEI 215 x TZdEI 238 had a significant positive mid-parent heterosis of 5.24% for days to anthesis. The hybrids TZEI 472 x TZEI 470 and TZdEI 215 x TZdEI 238 were the only crosses with significant mid-parent heterosis of 6.0 % and 6.2% for days to silking, respectively. Similarly, TZdEI 215 x TZdEI 238 was the only hybrid with a significant positive better-parent heterosis of 5.24% for days to silking (Appendix 11).

6.3.2 Heterosis for grain yield and its component traits in early maturing hybrids

under low soil nitrogen environments

Under low-N, significance for both MPH and BPH were obtained for days to anthesis and ssilking, plant and ear heights, root lodging, stalk lodging, plant aspect, ears per plant, and stay green characteristic (Appendix 11). TZEI 497 x TZEI 520 was the only hybrid with significant heterosis for days to anthesis and silking. It had significant positive mid-parent heterosis of 6.72% and 8.36% for days to anthesis and days to silking, respectively. The hybrids TZEI 461 x TZEI 462 (37.41%), TZEI 379 x TZEI 298 (42.21%), TZEI 462 x TZEI 8 (50.24%), TZEI 298 x TZEI 365 (63.08%), TZdEI 283 x TZEI 298 (69.44%) and TZdEI 272 x TZdEI 124 (75.51%) were crosses with significant mid-parent heterosis for root lodging (Appendix 11). The hybrids TZdEI 216 x TZEI 298 (-37.71%), TZdEI 283 x TZEI 298 (60.19%), TZEI 298 x TZEI 365 (60.33%), TZdEI 272 x TZdEI 124 (74.20%) had significant better-parent heterosis for root lodging. The hybrids TZdEI 283 x TZEI 298, TZEI 298 x TZEI 365 and TZEI 470 x TZEI 520 had significant mid-parent and betterparent heterosis for stalk lodging. TZEI 497 x TZEI 520 was the only hybrid with significant heterosis for plant aspect under low-N environments with a positive mid-parent heterosis estimate of 24.53%. The hybrid TZEI 298 x TZEI 365 had mid-parent and betterparent heterosis of 84.06% and 78.53% for ears per plant, respectively. Similarly, TZdEI 272 x TZdEI 124 and TZEI 3A x TZdEI 124 were the only hybrids with significant midparent and better parent heterosis for stay green characteristic: the hybrid TZdEI 272 x TZdEI 124 had significant negative mid-parent and better parent heterosis estimates of 36.40% and -41.50%, respectively, while TZEI 3A x TZdEI 124 had significant positive estimates for mid-parent and better-parent heterosis of 20.25% and 19.59% for stay green characteristic, respectively. The hybrid TZEI 497 x TZEI 520 had significant estimates of

-23.51% and -28.91% for mid-parent and better-parent heterosis for ear height, respectively, and -21.90% and -25.31% for mid-parent and better-parent heterosis for plant height, respectively. A significant negative mid-parent heterosis of -20.27% for plant height was also recorded by TZEI 468 x TZEI 467, while TZEI 456 x TZEI 449 had a significant positive mid-parent heterosis of 26.05% for ear height (Appendix 11).

6.3.3 Heterosis for grain yield and its component traits in early maturing hybrids under *Striga*-infested environments

The heterosis estimates for most traits measured under *Striga*-infested environments were relatively higher than estimates of the same traits measured in the other environments (Data not shown). The only significant mid-parent and better-parent heterosis for grain yield under *Striga*-infested environments was recorded by TZEI 127 x TZEI 449. It produced 83.02% more grains over the mid-parent value and 73.06% more grain over the better parent. The estimates for both mid-parent and better-parent heterosis for anthesis-silking interval for all the 150 hybrids were significant and negative (Appendix 12). The midparent heterosis for anthesis-silking interval ranged from -42% for TZEI 468 x TZEI 462 to -66.25% for TZEI 475 x TZEI 468. The hybrid TZEI 379 x TZEI 3A recorded the lowest better-parent heterosis of -47.22% for anthesis-silking interval, while TZdEI 272 x TZdEI 124 recorded the highest better-parent heterosis of -68.03%. The hybrids TZEI 485 x TZEI 127 and TZdEI 283 x TZdEI 272 were the only two hybrids with significant negative heterosis for plant height under *Striga*-infested environments: a mid-parent heterosis of 19.18% and a better-parent heterosis of -23.49% were recorded by TZEI 485 x TZEI 127. TZdEI 283 x TZdEI 272 recorded MPH and BPH estimates of -22.45% and 22.63%, respectively. About 76% of the hybrids evaluated had significant mid-parent and

betterparent heterosis for number of emerged *Striga* plants at 8 WAP. The lowest mid-parent heterosis of 74.8% for number of emerged *Striga* plants at 8 WAP was recorded by TZEI

470 x TZEI 461, while the highest mid-parent heterosis of 478.45% for number of emerged *Striga* plants at 8 WAP for TZEI 376 x TZdEI 216. The better-parent heterosis ranged from 77.81% for TZEI 402 x TZdEI 192 to 458.42% for TZEI 376 x TZdEI 216. The hybrids TZdEI 238 x TZdEI 216, TZdEI 192 x TZEI 379, TZdEI 272 x TZEI 376 and TZdEI 272 x TZdEI 192 were the only hybrids with non-significant estimates for mid-parent and better-parent heterosis for number of emerged *Striga* plants at 8 WAP. The mid-parent heterosis for number of emerged *Striga* plants at 10 WAP ranged from 79.55% for TZdEI 69 x TZEI 3A to 1316.31% for TZdEI 69 x TZdEI 272. The better-parent heterosis for number of emerged *Striga* plants at 10 WAP ranged from 76.61 for TZEI 378 x TZEI 298 to 1135.88% for TZdEI 69 x TZdEI 272.

6.3.4 Heterosis for grain yield and its component traits in early maturing hybrids across optimal growing conditions, *Striga*-infested and low-N environments

Non-significant mid-parent and better parent heterosis were observed for all the 150 hybrids for all traits measured across the three research environments.

6.4 Discussion

It has been observed that *per se* performance of inbred parents usually do not correlate with performance of their hybrids. Therefore, to know the precise genetic worth of inbred lines in hybrid combination, it is worthy to know the magnitude of heterosis for grain yield and for any other desired traits of potential parents for hybrid development. In the present study,

the magnitude of both mid-parent and better-parent heterosis were very low for most traits under low-N and optimal environments, and highest under *Striga*-infested environments. This could be attributed to the relatively large SCA effects over GCA effects of most of the parent lines under *striga*-infested environments as compared to their effects in other research environments (Mulualem and Abate, 2016). The heterosis expressed by most of the hybrids were not statistically significant under the three research environments, and particularly across environments. Similarly, low levels of significant heterotic effects were reported by Dhoot *et al.* (2017) and Kumar *et al.*, (2014) for grain yield and its component traits. In general, the magnitude of both mid-parent and better-parent heterosis for most traits were higher for hybrids of parental lines from different heterotic groups identified by the SNP-GD heterotic grouping method. This was particularly the case of hybrids TZEI 127 x TZEI 449 (grain yield), TZEI 475 x TZEI 468 (ASI), TZEI 485 x TZEI 127 (plant height), TZEI 376 x TZdEI 216 (number of emerged *Striga* plants at 8 WAP) that expressed significant heterosis for traits under *Striga*-infested environments. Similarly, hybrids of parents from different heterotic groups such as TZdEI 283 x TZEI 298 (stalk and root lodging), TZEI 462 x TZEI 8 and TZdEI 216 x TZEI 298 (root lodging), TZEI 497 x TZEI 520 (days to silking and anthesis, and plant and ear height, plant aspect) and TZEI 3A x TZdEI 124 (stay green characteristic) also obtained significant heterosis under low-N environments, and TZdEI 215 x TZdEI 238 for mid-parent and better-parent for days to anthesis and silking under optimal growing conditions. This result corroborated the findings that heterosis in maize increase with increased genetic divergence of the parent populations (Moll *et al.*, 1962).

The non-significant mid-parent and better-parent heterosis in most of the hybrids for most traits under optimal, *Striga*-infested, low-N environments and across environments indicated that any magnitude of superiority or inferiority in performances of those hybrids over their parents were not reliable differences and could be due to other phenomena other than heterosis (Hallauer, 1997). On the contrary, the significant heterosis observed in some hybrids for traits under each and across environments indicated reliable differences in the relative performance of those hybrids over their parents and their potential usefulness in breeding programs. In the present study, heterosis in negative direction for days to anthesis and silking, anthesis-silking interval, root lodging, stalk lodging, husk cover, plant and ear aspects, ears per plant, stay green characteristic, *Striga* damage syndrome ratings at 8 and 10 WAP were considered desirable. For traits like grain yield and ears per plant positive heterosis were desirable, while for plant and ear heights and number of emerged *Striga* plants at 8 and 10 WAP both positive and negative heterosis were desirable. The significant positive mid-parent and better-parent heterosis for days to anthesis and silking exhibited by TZdEI 215 x TZdEI 238 under optimal environments indicated a significant delay in the flowering of the hybrids as compared to the earliness in silking of both parents. The hybrid TZEI 472 x TZEI 470 also exhibited significantly higher number of days to silking than the average number of days taken by both parents to silk. The expression of lateness in flowering by TZdEI 215 x TZdEI 238 and TZEI 472 x TZEI 470 under optimal growing conditions may not be desirable as the target of this study was to develop early maturing varieties, however late flowering will probably not have any adverse effects on grain yield of the hybrids under optimal growing conditions (Sharifi and Namvar, 2016)).

Under low-N environments, the significance of negative mid-parent and better-parent heterosis of plant and ear heights expressed by TZEI 497 x TZEI 520 indicated that the hybrid had shorter plant and ear heights when compared to the average plant and ear heights of both parents and for even the tallest parent. The reduction in height of averagely 24.91% of the inbred parents is desirable since extremely tall plants are prone to lodging with adverse effects on grain yield. Under low-N environments, the significant mid-parent and better-parent heterosis for ears per plant by TZEI 298 x TZEI 365 indicated that the hybrid produced more ears per plant than the average number of ears per plant produced by both parents and even by the parent with highest number of ears per plant. This makes TZEI 298 x TZEI 365 a very desirable cross, and would be very useful under low-N environments since increased number of ears per plant is a good indicator of improved grain yield under low-N environments (Bänziger *et al.*, 2000). The hybrid TZdEI 272 x TZdEI 124 expressed significantly negative mid-parent and better parent heterosis for stay green characteristic, which showed that TZdEI 272 x TZdEI 124 had delayed leaf senescence under low-N environments and the leaf of the parental inbred lines senesced faster than this hybrid. The expression of reduced leaf senescence under low-N environments is very desirable as delayed senescence is a key component of nitrogen use efficiency in maize (Bänziger *et al*., 2000).

In this study, the hybrid TZEI 127 x TZEI 449 was the only one out of the 150 hybrids to express significant heterosis for grain yield. It produced 83.02% more grains over the average grain yield of both parents and 73.06% more grain over the better-parent under *Striga*-infested environments. This makes TZEI 127 x TZEI 449 a very desirable hybrid for *Striga*-infested environments. The significant negative mid-parent and better-parent

heterosis for anthesis-silking interval of all the 150 hybrids under *Striga*-infested environment showed improved synchronization of the male and female flowers of the hybrids resulting in relatively shorter days from anthesis to silking than the average days taken by both parents and even for the better parent. The reduction in anthesis-silking interval for almost all the hybrids under *Striga*-infested environments is striking, since reduction in anthesis-silking interval of maize under stress is a good indication of stress tolerance and improved yield (Badu-Apraku and Fakorede, 2017). The hybrids TZEI 485 x TZEI 127 and TZdEI 283 x TZdEI 272 were desirable for displaying significantly reduced plant height than the average plant heights of their parents under *Striga*-infested environments. The significant positive number of emerged *Striga* plants at 8 and 10 WAP by most of the hybrids indicated that they supported more number of emerged *Striga* plants than the average number supported by their parents. The increased number of emerged *Striga* plants of the hybrids than their parents per se do not suggest that the hybrids are susceptible to *Striga* infestation, it could also mean that they are tolerant to *Striga* if they produce more yields than their parents and local checks used in this study. Therefore, the 76% to 98% of hybrids with significantly positive mid-parent and better-parent heterosis for number of emerged *Striga* plants at 8 and 10 WAP should be further tested for superior grain yield performance and other *Striga* adaptive traits.

CHAPTER SEVEN

7.0 Evaluation of grain yield potential and stability of early maturing single-cross hybrids across contrasting environments

7.1 Introduction

Maize production in Ghana and the rest of SSA is very low, averaging 1.81t ha^{-1} (FAOSTAT, 2013). The low yields in SSA is attributed in part to production constraints such as drought, low soil nitrogen, *Striga hermonthica* infestation, and low use of improved varieties (Gibbon *et al*., 2007). It is believed that although crop management interventions may have a greater potential for significant impact on maize production in marginal environments than genetic solutions, stress-tolerant germplasm will be the most economical and faster to be adopted by farmers than agronomic interventions (Heisey and Edmeades, 1999). For stress tolerance breeding programs, it is recommended that fields for screening of germplasm should be selected and managed with the aim to simulate a clearly defined stress that is relevant to farmers' fields (Bänziger *et al*., 2000). It is also recommended that variety trials should be conducted at several locations in different years to enhance the chances of identifying superior and stable genotypes for target environments (Yan *et al*., 2007).

Genotype x environment interaction (GEI) refers to the differential ranking of genotypes across a range of environments (Allard and Bradshaw, 1964; Kang, 1998). Generally, GEI complicates the selection of genotypes that may do well over diverse environments. The presence of biotic (*Striga*) and/or abiotic (Low-N and drought) stresses compound GEI

effects probably due to the complexities in the genetics of resistance/tolerance of a crop variety to stress (Akinwale *et al*, 2013.). The presence of large GEI indicates that differences in yields among genotypes will depend on the environment (Yue *et al*., 1997). Consequently, selection procedures based on the mean yield of cultivars in a given environment are less efficient (Hopkins *et al*., 1995, Scapim *et al*., 2000). the most efficient strategy employed by breeders' to develop cultivars with diminished GEI is to select genotypes with better stablilty across wide range of environments to better predict the response of a genotype to targeted environments (Eberhart and Russell, 1966; Tai, 1971, Babic *et al.,* 2010). Various methods use the G x E interaction to facilitate genotype characterization and as a selection index together with the mean yield of the cultivars. Among such methods is the GGE biplot which is considered as the most powerful method to explore GEI patterns (Yan and Tinker, 2006). The GGE biplot captures both genotype main effects and GEI effects (Yan *et al.*, 2001), and graphically presents them in a way that facilitates visual evaluation of genotypes and mega-environment identification in multi-environment trials (METs) (Yan *et al*., 2000).

The broad objective of this study was to determine the yield potential and stability of the 150 early maturing single-cross hybrids of North Carolina design II crosses involving 30 inbred parents under optimal growing conditions, low-N, *Striga*-infested and across environments.

The specific objectives of the study were to:

i. Assess the yield response of the hybrids under low-N, *Striga*-infested and optimal environments, ii. Identify the most suitable environments for the best performing

hybrids, iii. Identify the best testing environments for selection of superior and stable hybrids.

7.2 Materials and methods

7.2.1 Genetic materials

The 150 single-cross hybrids and six local checks described in Chapter 5 Section 5.2.1 were used in this study.

7.2.2 Field procedures

The hybrids were evaluated under optimal growing conditions, low-N and *Striga*-infested environments as described in Chapter 5 Section 5.2.2.

7.2.3 Data collection

The grain yield data used in this study were the same as described in Chapter 5 Section 5.2.2.

7.2.4 Data analysis

Genotype main effect plus genotype × environment interaction (GGE) biplot analysis of the yield data of the hybrids was performed to evaluate the yield response and stability of the hybrids across the ten test environments presented in Tale 7.1. Based on the mean grain yields of the hybrids under *Striga*-infested, low-N and optimal environments (Appendix 13), the yield data of the best 30 and worst 10 hybrids across *Striga*-infested and *Striga*free environments, low- and high-N environments and *Striga*-infested, low-N and optimal environments (*Striga*-free and high-N environments) were subjected to GGE biplot analysis. The GGE biplot pattern explorer version 8.0 (Yan, 2001) was used. The GGE biplot model equation used is as follows:

$$Y_{ij} - Y_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{j2} \eta_{j2} + \Sigma_{ij}$$

Where, Y_{ij} is the average yield of genotype i in environment j,
Y_j is the average yield across all genotypes in environment j, λ_1 and λ_2 are the singular values for principal components PC1 and PC2, ξ_{i1} and ξ_{j2} are the PC1 and PC2 scores for genotype i, $\eta_{j1}$and η_{j2} are the PC1 and PC2 scores for environment j and

Σ_{ij} is the residual of the model associated with the genotype i in environment j.

The data were not transformed (Transform=0), not standardized (Scale=0) and were environment-centered (Centering=2).

The formula below was used to calculate percentage grain yield reduction or increase of the hybrids resulting from *Striga* parasitism and nitrogen deficiency (stress).

$$YRED\ (\%) = \frac{Grain\ yield\ under\ stress}{Grain\ yield\ under\ non-stress} X\ 100$$

Where YRED is percentage yield reduction/increase due to stress.

Table 7. 1 Names and codes of test environments used in this study

Environment	Research Condition	Year	Location
MOK-NSTR-16	Optimal (*Striga*-free)	2016	Mokwa
NYK-NSTR-17	Optimal (*Striga*-free)	2017	Nyankpala
KWD-HN-16	Optimal (High-N)	2016	Kwadaso
KWD-HN-17	Optimal (High-N)	2017	Kwadaso
MOK-STR-16	*Striga*-infested	2016	Mokwa
NYK-STR-16	*Striga*-infested	2016	Nyankpala
MAN-STR-16	*Striga*-infested	2016	Manga
NYK-STR-17	*Striga*-infested	2017	Nyankpala
KWD-LN-16	Low nitrogen	2016	Kwadaso
KWD-LN-17	Low nitrogen	2017	Kwadaso

7.3 Results

7.3.1 Grain yield performance of the early maturing hybrids across *Striga*-infested, low-N and optimal environments

The average yield of the hybrids across the ten test environments was 3490 kg ha^{-1}. The hybrid TZEI 376 x TZdEI 69 produced the highest yield of 6523 kg ha^{-1}. The yield of the hybrids under low-N environments ranged from 452 kg ha^{-1} to 5313 kg ha^{-1}, while the yield under optimal environments ranged from 1724 kg ha^{-1} to 11,679 kg ha^{-1}. The average yield reduction due to nitrogen stress was 46.87% of the yield recorded under optimal environments (Appendix 13). The highest grain yield under *Striga* infestation was 4546 kg ha^{-1} and was produced by TZEI 127 x TZEI 449, while the lowest yield (980 kg ha^{-1}) was produced by the local check 1(Kunjor- Wari). The average yield reduction due to *Striga* parasitism was 51.79 % of the average yield recorded under optimal environments (Appendix 13).

7.3.2 GGE biplot analysis of grain yield and stability of selected early maturing hybrids across low-N and high-N environments

In Figures 7.1 and 7.2, the principal component axis 1(PC1) explained 61.3% of the total variation in grain yield of the hybrids across low-N and high-N environments while principal component axis 2 (PC2) explained 18.5% and, thus the two axes accounted for 79.8% of the total variation for grain yield across low and high-N environments. The 'Which -won-Where' GGE biplot for grain yield of the best 30 and worst 10 yielding hybrids (Table 7.2) evaluated across low-N and high-N environments in 2016 and 2017 is presented in Figure 7.1. The polygon view of this GGE biplot was constructed to show

which hybrids performed best in which environment. The vertex genotype in each sector represents the highest yielding hybrid in the environment that falls within that sector (Yan *et al.,* 2005; 2010). Entry E47 was the highest yielding hybrid at KWD-HN-17 and KWDLN-17. Entry E106 was the best for KWD-LN-16 and KWD-HN-16. The hybrids E140,

E126 and E29 were also among the highest yielders in KWD-LN-16 and KWD-HN-16. On the contrary, the vertex hybrids, E84, E99, E135, E48 and E50 were the lowest yielding hybrids at all or some environments and thus, no environments fell into the sectors with those hybrids. Furthermore, the hybrids within the sectors such as E90, E54, E17, E77, E28 and E51 were less responsive than the vertex hybrids. The Mean vs. Stability view of the GGE biplot based on yield data of the selected hybrids across low-N and high-N is presented in Figure 7.2. The biplot is interpreted below according to the following terminologies as defined by Yan (2001). The average environment is indicated by the small circle in Figure 3.5.2, which is a virtual environment defined by the average coordinates of all environments to represent the target environment. The average environment axis (AEA) is the single-arrowed line in the biplot that passes through the biplot origin and the average environment. The average environment coordinate (AEC) is the coordination with the AEA as the abscissa. The AEC ordinate is the double arrowed line, which passes through the biplot origin and is perpendicular to the AEA. The AEC ordinate has two arrows, pointing outward from the biplot origin. The arrows point to higher instability for the hybrids regardless of the direction. Based on the above information, E31, E47, E72, E73 and E147 were ranked as the top five hybrids with the highest mean yields across low-N and high-N

test environments (Table 7.1). The entries E136, E84, E50, E48 and E135 were ranked as the lowest yielding hybrids across low and high N environments. The hybrids E140, E106, E126, E29, E107, E38 and E147 were high yielding and highly unstable, while E110, E50, E136 were low yielding and unstable. The entries E72 and E18 were the highest yielding and most stable hybrids. The entries E56 and E48 were low yielding and very stable across the four test environments (Table 7.1).

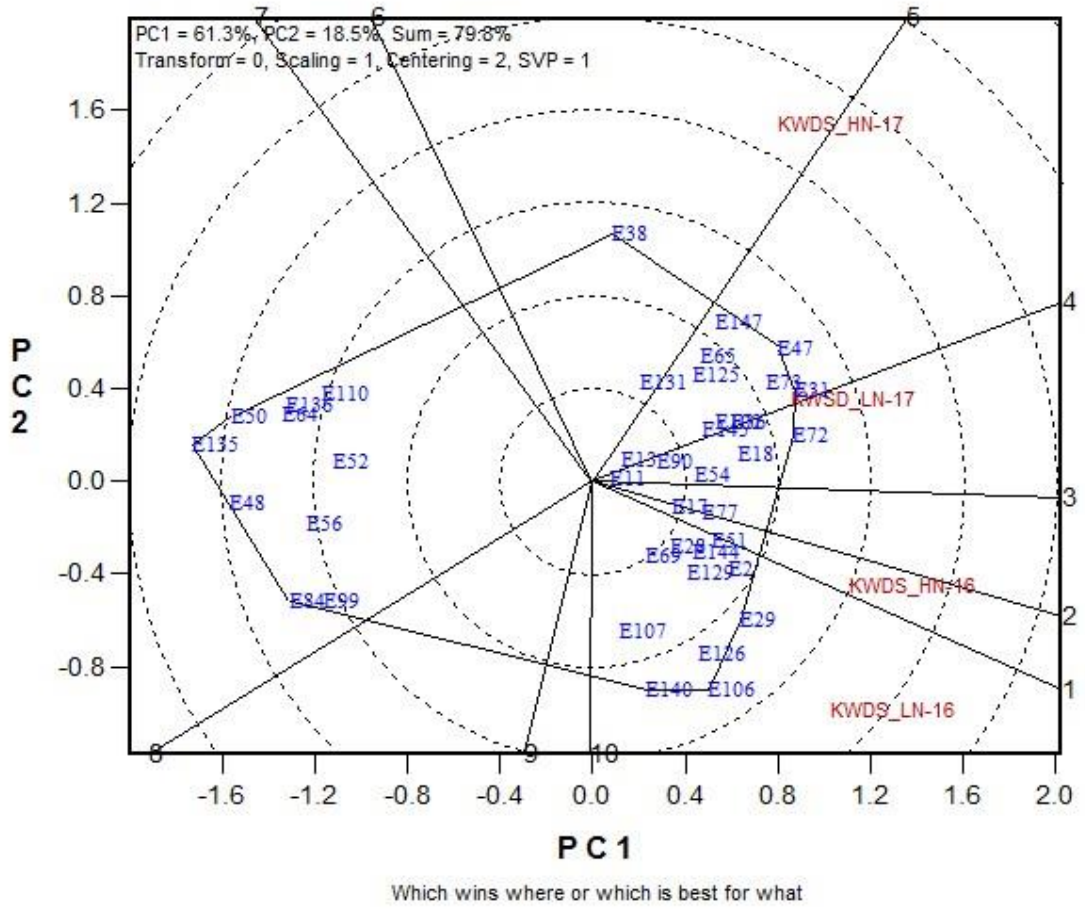

Figure 7. 1 A 'which won where' GGE biplot based on a genotype × environment yield data of the best 30 and worst 10 yielding early maturing maize hybrids evaluated across low-N and high-N environments in 2016 and 2017

Table 7. 2 Name and code of hybrids used in GGE biplot analysis for each contrasting environment

Hybrid name	Code	Hybrid name	Code	Hybrid name	Code
Across low and high N environments					
TZEI 127 x TZEI 449	E31	TZdEI 215 x TZEI 365	E77	TZEI 449 x TZEI 520	E52
TZdEI 124 x TZdEI 283	E72	TZdEI 69 x TZdEI 215	E54	TZEI 470 x TZEI 520	E110
TZEI 127 x TZEI 497	E47	TZEI 468 x TZEI 127	E145	TZEI 467 x TZEI 470	E56
TZEI 378 x TZdEI 215	E73	TZEI 376 x TZdEI 69	E129	TZdEI 283 x TZEI 3A	E99
TZdEI 216 x TZdEI 272	E18	TZEI 379 x TZdEI 215	E17	TZEI 468 x TZEI 472	E136
TZdEI 215 x TZdEI 124	E36	TZEI 8 x TZEI 520	E144	TZEI 470 x TZEI 468	E84
TZdEI 192 x TZdEI 216	E29	TZdEI 283 x TZdEI 215	E90	TZEI 461 x TZEI 462	E64
TZdEI 124 x TZEI 379	E2	TZEI 3A x TZdEI 192	E28	TZdEI 283 x TZEI 298	E50
TZEI 378 x TZdEI 272	E102	TZEI 379 x TZdEI 272	E140	TZEI 475 x TZEI 461	E48
TZdEI 215 x TZdEI 192	E126	Check 2 - SUHUDOO	E131	TZEI 472 x TZEI 470	E135
TZdEI 272 x TZdEI 192	E106	TZdEI 40 x TZEI 472	E38	TZdEI 272 x TZdEI 124	E107
TZEI 456 x TZEI 449	E147	TZdEI 216 x TZEI 298	E13	TZdEI 69 x TZdEI 272	E11
TZEI 449 x TZdEI 40	E65	TZdEI 192 x TZEI 379	E69		
TZEI 365 x TZdEI 216	E125	TZEI 467 x TZEI 449	E51		
Across *Striga*-infested and *Striga*-free environments					
TZEI 376 x TZdEI 69	E129	TZEI 470 x TZdEI 40	E3	TZEI 402 x TZdEI 192	E112
TZEI 379 x TZdEI 215	E17	TZdEI 40 x TZEI 456	E44	TZdEI 238 x TZdEI 283	E45
TZdEI 124 x TZEI 379	E2	TZdEI 216 x TZEI 402	E10	TZdEI 69 x TZEI 402	E14
TZEI 8 x TZdEI 40	E138	TZdEI 215 x TZdEI 124	E36	TZdEI 192 x TZEI 379	E69
TZEI 461 x TZEI 127	E58	TZdEI 215 x TZEI 376	E93	TZEI 402 x TZdEI 124	E92
TZEI 127 x TZEI 449	E31	TZdEI 215 x TZdEI 192	E126	TZdEI 216 x TZdEI 215	E19
TZEI 379 x TZdEI 272	E140	TZdEI 283 x TZEI 298	E50	TZEI 462 x TZEI 497	E86
TZdEI 40 x TZEI 462	E32	TZdEI 283 x TZdEI 215	E90	TZEI 449 x TZEI 520	E52
TZEI 378 x TZdEI 272	E102	TZdEI 272 x TZdEI 238	E20	TZEI 467 x TZEI 470	E56
TZdEI 124 x TZEI 378	E68	TZEI 8 x TZEI 485	E62	TZEI 461 x TZEI 456	E85
TZEI 378 x TZdEI 215	E73	TZdEI 192 x TZEI 378	E81	TZEI 520 x TZEI 467	E95
TZdEI 69 x TZdEI 215	E54	TZEI 475 x TZEI 461	E48	TZEI 468 x TZEI 467	E151
TZdEI 272 x TZdEI 124	E107	TZEI 497 x TZEI 520	E119		
TZdEI 40 x TZEI 127	E33	TZEI 298 x TZEI 376	E127		
Across optimal, *Striga*-infested and low-N environments					
TZEI 376 x TZdEI 69	E129	TZEI 470 x TZdEI 40	E3	TZEI 402 x TZdEI 192	E112
TZEI 379 x TZdEI 215	E17	TZdEI 40 x TZEI 456	E44	TZdEI 238 x TZdEI 283	E45
TZdEI 124 x TZEI 379	E2	TZdEI 216 x TZEI 402	E10	TZdEI 69 x TZEI 402	E14
TZEI 8 x TZdEI 40	E138	TZdEI 215 x TZdEI 124	E36	TZdEI 192 x TZEI 379	E69
TZEI 461 x TZEI 127	E58	TZdEI 215 x TZEI 376	E93	TZEI 402 x TZdEI 124	E92
TZEI 127 x TZEI 449	E31	TZdEI 215 x TZdEI 192	E126	TZdEI 216 x TZdEI 215	E19

TZEI 379 x TZdEI 272	E140	TZdEI 283 x TZEI 298	E50	TZEI 462 x TZEI 497	E86
TZdEI 40 x TZEI 462	E32	TZdEI 283 x TZdEI 215	E90	TZEI 449 x TZEI 520	E52
TZEI 378 x TZdEI 272	E102	TZdEI 272 x TZdEI 238	E20	TZEI 467 x TZEI 470	E56
TZdEI 124 x TZEI 378	E68	TZEI 8 x TZEI 485	E62	TZEI 461 x TZEI 456	E85
TZEI 378 x TZdEI 215	E73	TZdEI 192 x TZEI 378	E81	TZEI 520 x TZEI 467	E95
TZdEI 69 x TZdEI 215	E54	TZEI 475 x TZEI 461	E48	TZEI 468 x TZEI 467	E151
TZdEI 272 x TZdEI 124	E107	TZEI 497 x TZEI 520	E119		
TZdEI 40 x TZEI 127	E33	TZEI 298 x TZEI 376	E127		

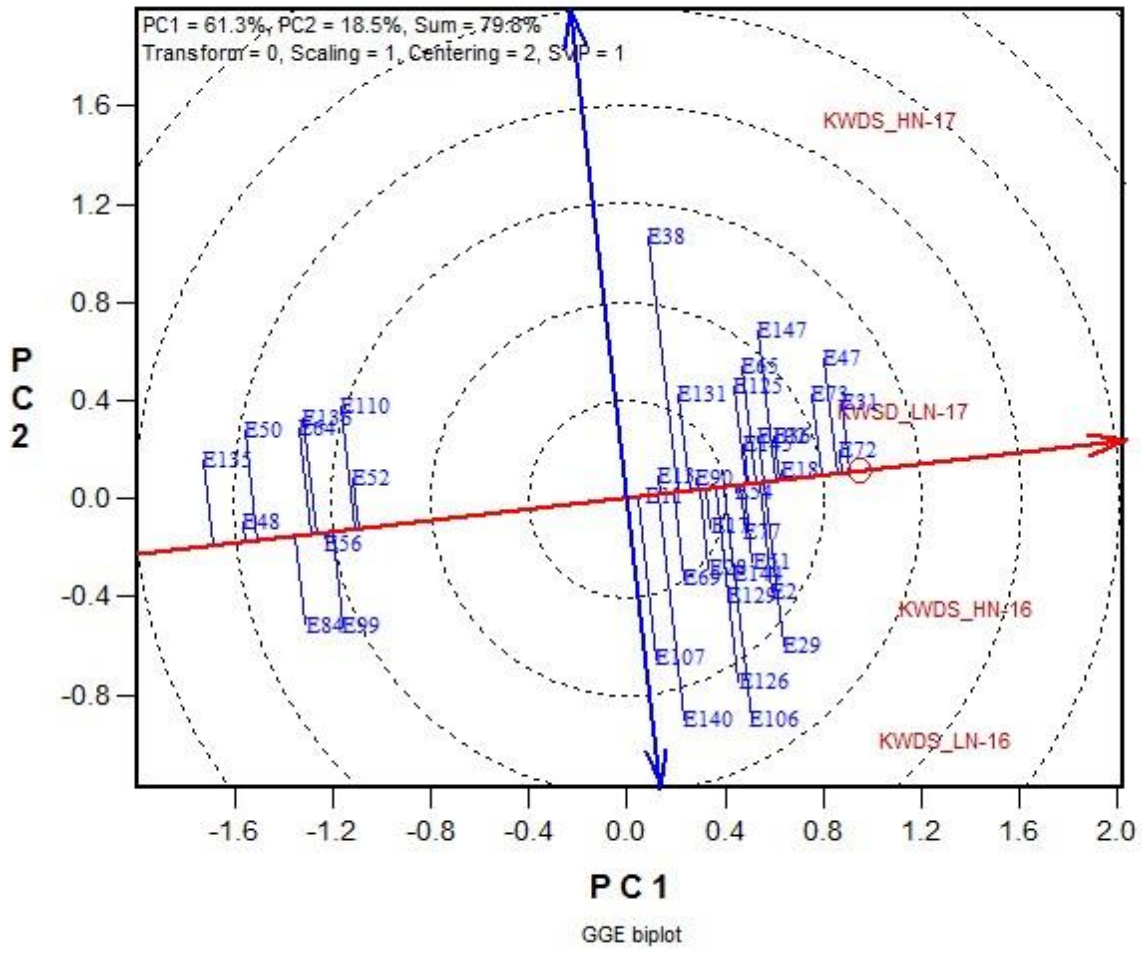

Figure 7. 2 The Mean vs. Stability view of the GGE biplot based on a genotype × environment yield data for grain yield of the best 30 and worst 10 grain yielding early maturing maize hybrids evaluated across low-N and high-N environments in 2016 and 2017

7.3.3 GGE biplot analysis of grain yield response and stability of selected early maturing hybrids across *Striga*-infested and *Striga*-free environments

The PC1 (43.2%) and PC2 (17.2%) of the biplots in Figures 7.3 and 7.4 explained 60.4% of the total variation for grain yield of the hybrids (Table 7.2 and Appendix 13) evaluated across *Striga*-infested and *Striga*-free environments. The hybrid E129 was the vertex hybrid where MOK-NSTR-16, NYK-NSTR-17 and MOK-STR-16 fell. The entry E31 was the vertex hybrid where NYK-STR-16, MAN-STR-16 and NYK-STR-17 fell.

Furthermore, E92, E69, E112, E46 and E3 and the other hybrids located within the sectors were less responsive than the vertex hybrids. The vertex hybrids, E15, E52 and E86 produced the lowest yield at all or some locations and thus, no environments fell into the sectors with those hybrids. The Mean vs. Instability GGE biplot in Figure 3.6.4 revealed that E31 and E109 were high yielding but highly unstable. Other high yielding hybrids such as E138, E81, E92, E19, E33 and E10 were also unstable. E81 was lower yielding and unstable, while E85 was low yielding but stable. The hybrids E68, E107, E102 and E119 were the highest yielding and most stable hybrids across *Striga*-infested and *Striga*-free environments.

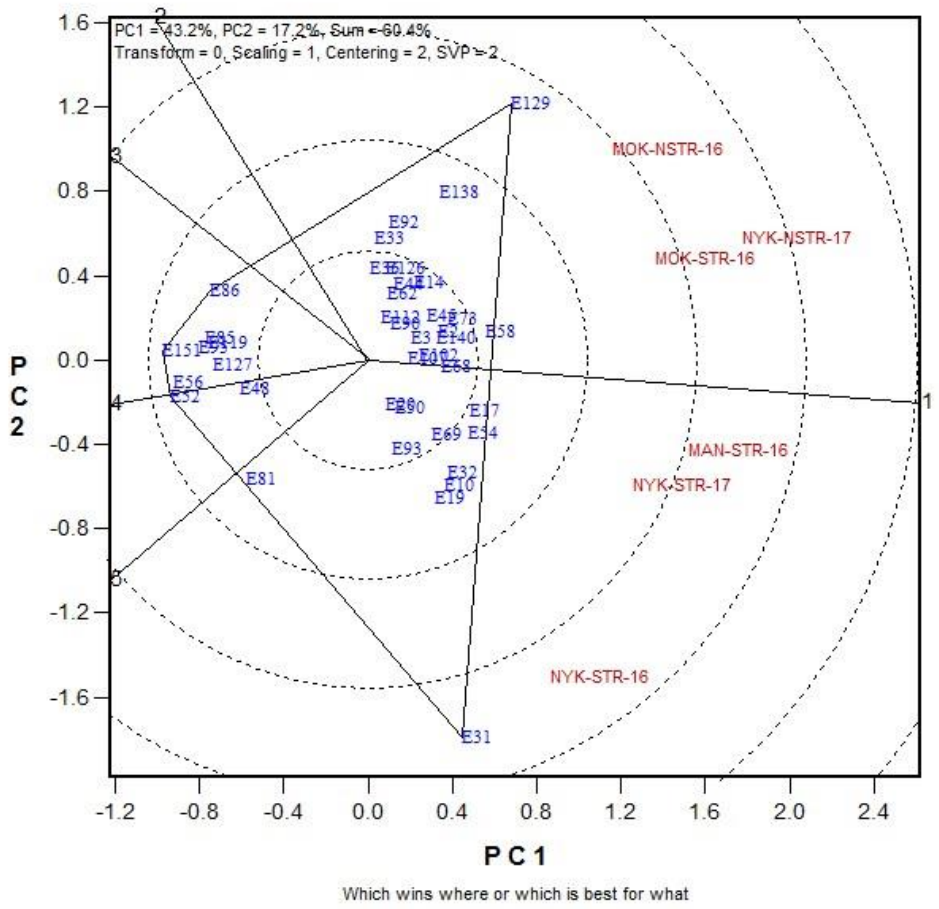

Figure 7. 3 A 'which won where' GGE biplot based on genotype × environment yield data of the best 30 and worst 10 yielding early maturing maize hybrids evaluated

across *Striga*-infested and *Striga*-free environments in 2016 and 2017

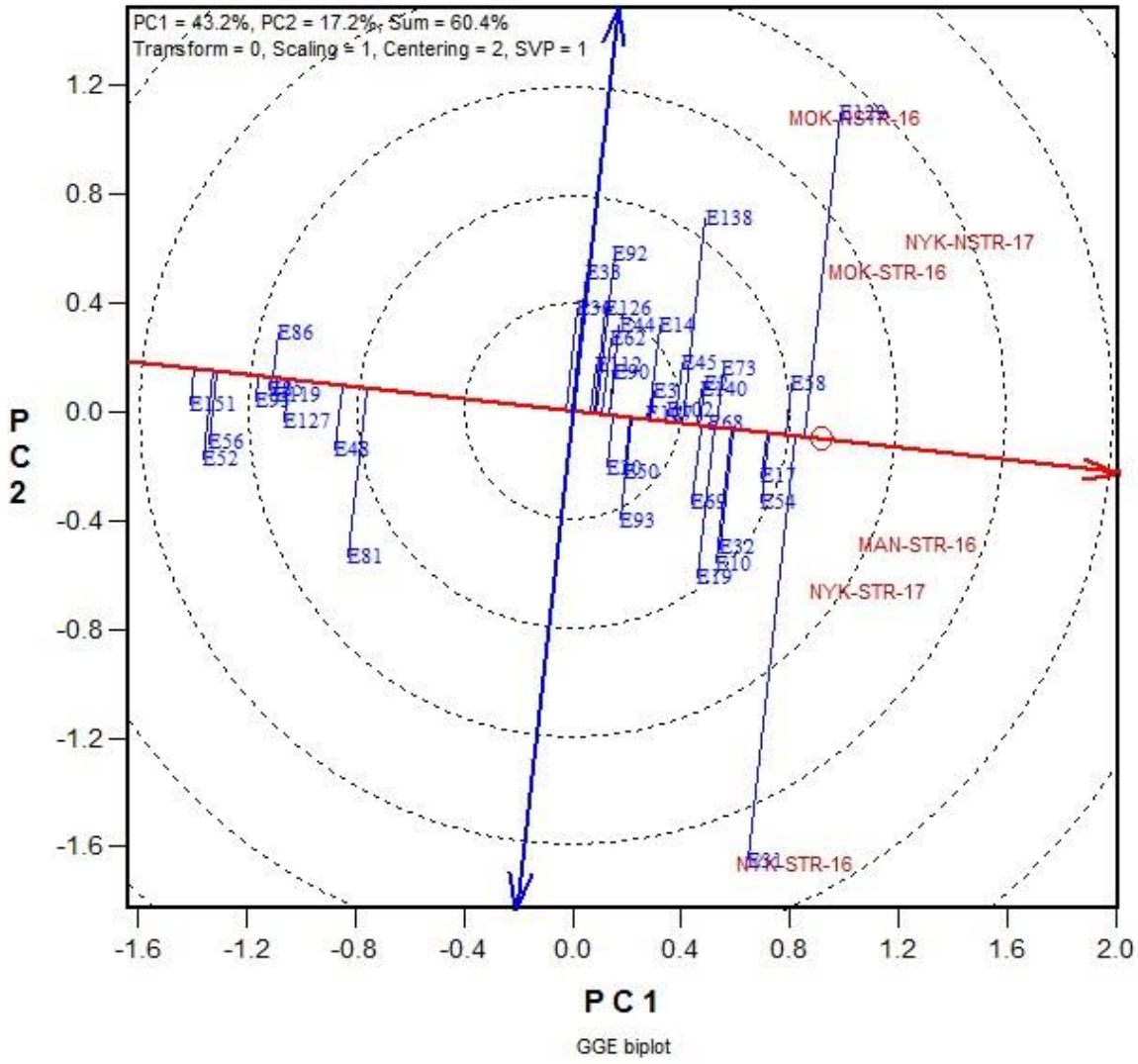

Figure 7. 4 The Mean vs. Stability view of the GGE biplot based on genotype × environment yield data for grain yield of the best 30 and worst 10 yielding early maturing maize hybrids evaluated across *Striga*-infested and *Striga*-free environments in 2016 and 2017

7.3.4 GGE biplot analysis of grain yield response and stability of selected early maturing hybrids across *Striga*-infested, low-N and optimal environments

In Figures 7.5 to 7.7, the PC1 explained 38.8% of total variation for grain yield of the hybrids across the three contrasting environments while PC2 explained 11.8% and, thus the two axes accounted for 50.6% of the total variation for grain yield of the hybrids across the ten test environments (Table 7.2 and Appendix 13). The entry E129 was the vertex hybrid where the environments KWD-HN-17, MOK-HN-16, KWD-LN-17, KWD-LN-16 and MOK-NSTR-16 fell. The entry E29 was the best hybrid for the environments MANSTR-16 and NYK-STR-16. The entry E31 was the best hybrid for the environments MOKSTR-16, NYK-NSTR-17 and NYK-STR-17. On the contrary, the vertex hybrids, E84, E36, E135, E48, E52 and E58 were the lowest yielding hybrids at all or some environments and thus, no environments fell in the sectors with those hybrids. The Mean vs. Stability GGE biplot of the hybrids across the ten test environments is presented in Figure 7.6. The biplot ranked the following hybrids as the top 10 performers across test environments: E129, E31,

E73, E2, E29, E54, E17, E140, E102, E69 and E72; while E84, E86, E127, E110, E135, E64, E151, E48, E52 and E56 were ranked as the lowest yielding hybrids across the test environments. The entries E84, E135 and E48 were not only low yielding but also highly unstable. Similarly, E129, E36, E18, E47, E58, E29 and E54 were high yielding and highly unstable across test environments. The high yielding and most stable hybrids across the test environments were E126, E73 and E28.

A vector view of GGE biplot showing the relationship among the test environments used for the evaluation of the selected hybrids is shown in Figure 7.7. The biplot in Figure 7.7 explained 85% of the total variation of the environment-centered G x E of the grain yield of the hybrids, and therefore it is appropriate for visualizing the relationship among the test environments. The lines that connect the test environments to the biplot origin are called environment vectors. The correlation between two environments is approximated by the cosine of the angle between their vectors. The presence of an acute angle indicates positive correlation, while an obtuse angle indicates a negative correlation. The presence of a right angle shows that the environments are not correlated. Based on these criteria, the following pair of environments, which had an angle between their vectors less than 90^{o} were strongly and positively correlated (KWD-HN-17 and MOK-NSTR-16; KWD-LN-17 and KWDLN-16; MOK-STR-16 and NYK-STR-17; MAN-STR-16 and NYK-STR-160, while the angle between vectors of environments MAN-STR-16 and KWD-LN-16 was approximately 90^{0}, and therefore those environments were not correlated (Figure 7.7). In Figure 7.7, the vector length of an environment measures its discriminating power to assess hybrids under the test environments that is, the longer the vector length the more discriminative the environment. Based on this information, the environments KWD-LN16, MAN-STR-16 and KWD-HN-16 had the longest vectors and thus were the most discriminating. The environments NYK-STR-16, NYK-STR-17 and KWD-LN-17 had the shortest vectors and were the least discriminating. In that same GGE biplot (Figure 7.7), the cosine of the angle between the vector of a test environment and the AEA approximates the genetic correlation between them and indicates the representativeness of the test environment i.e the smaller the angle the more representative the test environment is to the

AEA (Yan *et al.* 2011a). Thus, MOK-STR-16, was highly representative of the megaenvironment, followed by KWD-HN-16, NYK-STR-17, KWD-LN-16, NYK-NSTR-17 and KWD-LN-17, while MOK-NSTR-16 was moderately representative and MAN-STR16 was non-representative.

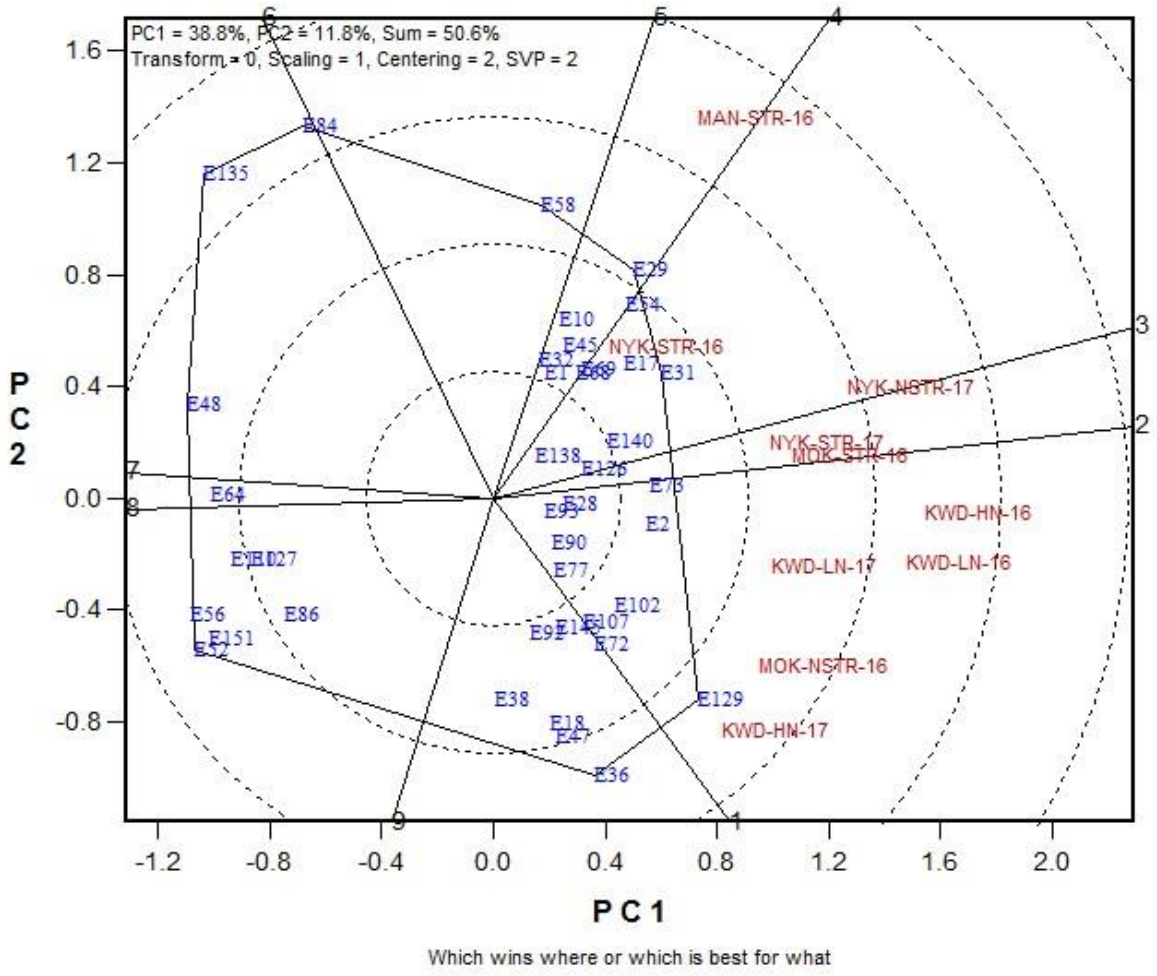

Figure 7. 5 A 'which won where' GGE biplot for grain yield of the best 30 and worst 10 yielding early maturing maize hybrids evaluated across *Striga*-infested, low-N and optimal environments in 2016 and 2017

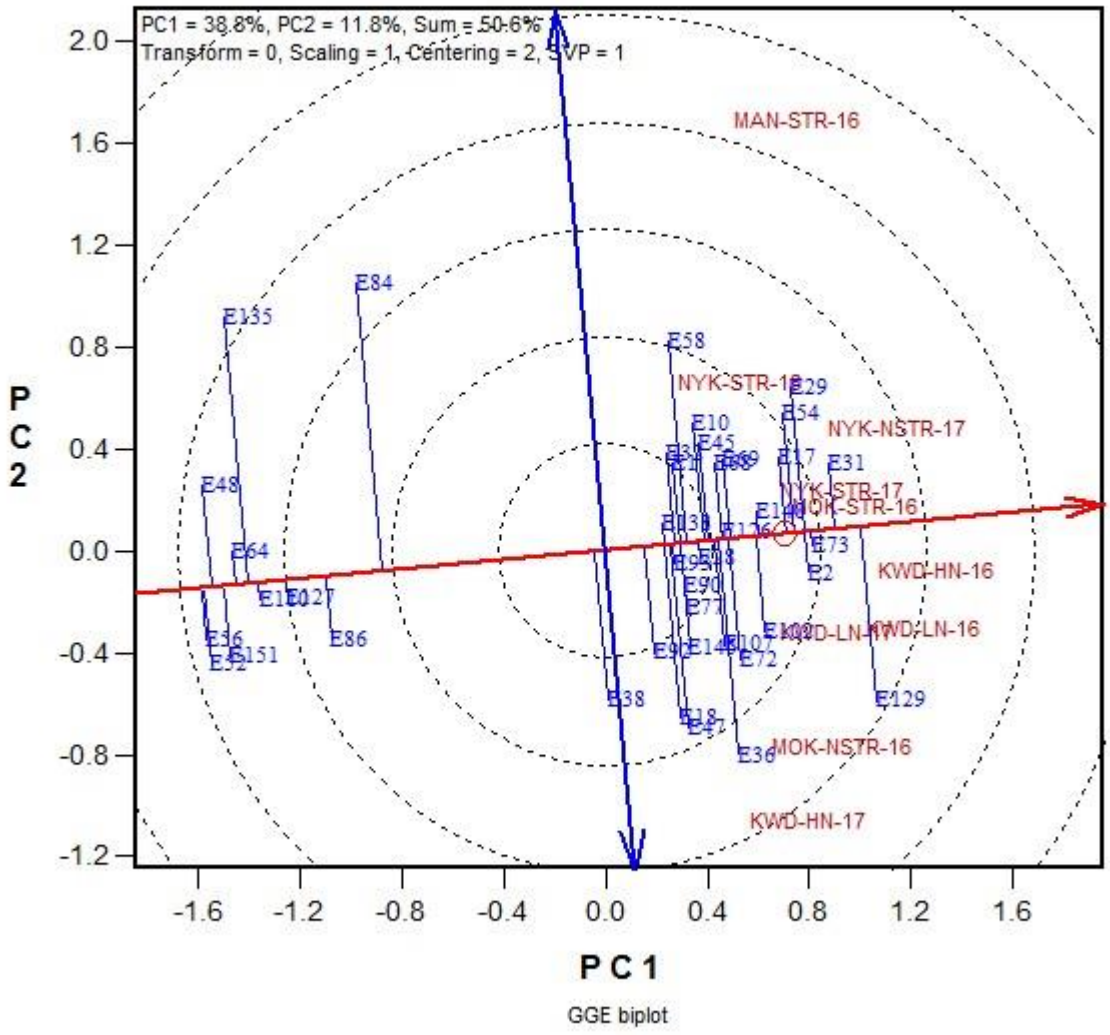

Figure 7. 6 A Mean vs. Stability view of the GGE biplot for grain yield of the best 30 and worst 10 yielding early maturing maize hybrids evaluated across *Striga*-infested, low-N and optimal environments in 2016 and 2017

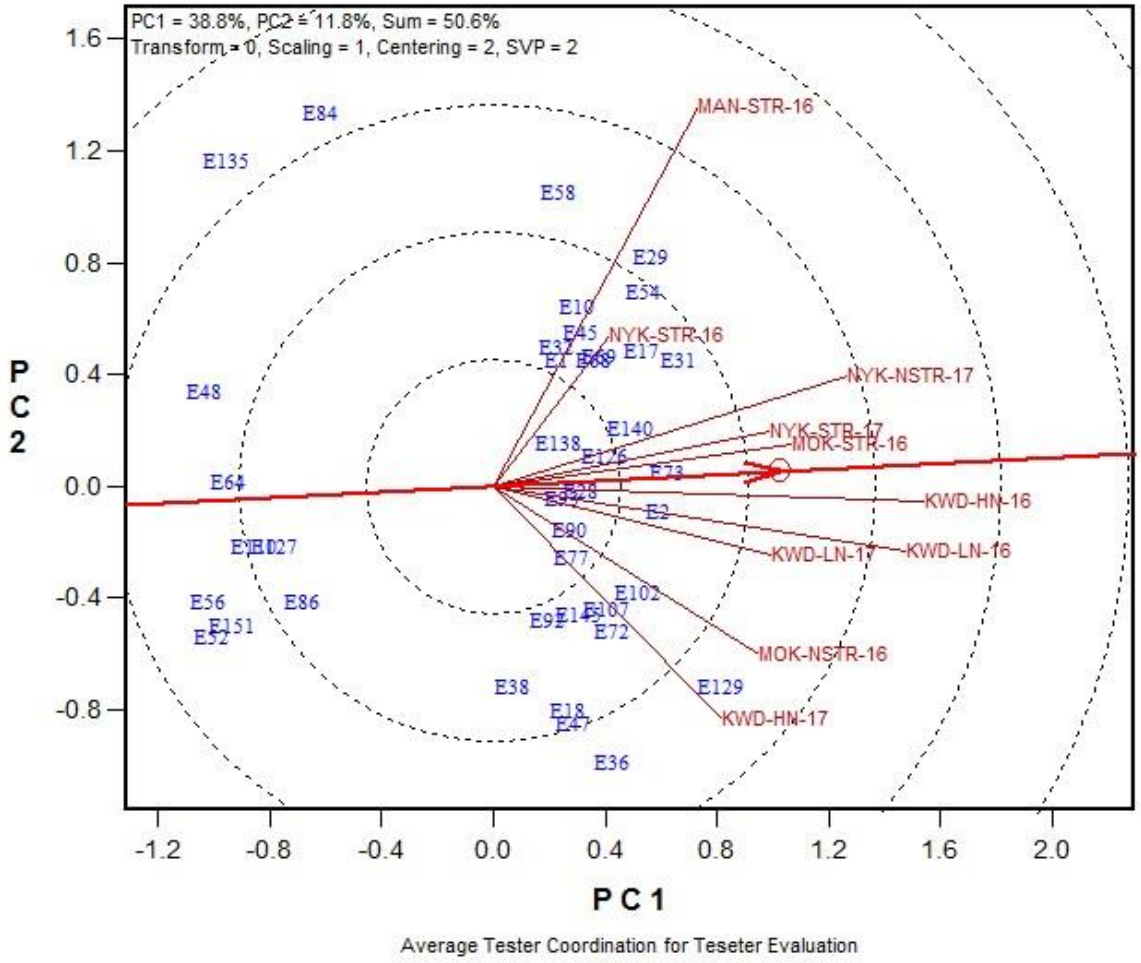

Figure 7. 7 A vector view of genotype plus genotype x environment biplot for grain yield of the best 30 and worst 10 early maturing maize hybrids evaluated across *Striga*-infested, low-N and optimal environments in 2016 and 2017

7.4 Discussion

In managed stress experiments, evaluation of genotypes under non-stress environment is generally required as a control to assess losses in yield potential associated with the stress. In the present study, the hybrids were most productive under optimal growing conditions, followed by low-N and *Striga*-infested environments. The magnitude of yield reduction due to a stress is indicative of whether the severity of the stress imposed in a study was severe enough to reveal genetic differences among the hybrids for that particular stress factor. According to Gallais and Coque (2005), the low N stress should be severe enough to cause a yield reduction of about 35-40% to be enough to reveal genetic difference between the genotypes. Therefore, the yield reduction of 46.7% recorded under low-N environments in this study was severe enough to discriminate the low N tolerant hybrids from the low N susceptible hybrids. Studies by the IITA extra-early and early maturing maize program has demonstrated that a yield reduction of 35-56% between *Striga*-infested and non-infested plots, is enough to allow separation of *Striga* tolerant genotypes from the susceptible ones (Badu-Apraku and Fakorede, 2017). It is therefore apparent that at 56.7% yield reduction, the stress intensity imposed in this study was severe enough to facilitate the discrimination of the *Striga* resistant hybrids from the susceptible hybrids.

Genotypic differences in grain yield observed when there is no stress are largely unrelated to differences observed when there is severe stress (Ceccarelli and Grando, 1991; Ceccarelli *et al*., 1992). Comparison of genotypic performance in contrasting environments provides the critical data required to predict yield stability of genotypes across target environments. Experiments conducted by Bänziger *et al*. (1997) and Presterl *et al*. (2003)

showed that phenotypic and genotypic correlations between grain yield under high and low nitrogen environments tend to decrease as the effect of N stress increases. Bänziger *et al*. (1997), reported a lower genetic correlation of 0.38 when the yield reduction at low N input was about 54%. Therefore, with a yield reduction of 46.87% due to low N and 51.76% due to *Striga* parasitism, it is evident that the yield performance of the hybrids would vary across the stress and non-stress environments used in this study. This implies that selection of the hybrids in the optimal environments for performance in either the *Striga*-infested or low-N environments would not be effective. For instance, the hybrids TZEI 376 x TZdEI 69, TZdEI 40 x TZEI 472, TZEI 378 x TZdEI 215, TZdEI 215 x TZdEI 192 and TZdEI 283 x TZdEI 215 ranked as the first five highest yielding hybrids under optimal environments were the 69th, 90th, 26th, 108th and 60th yielding hybrids, respectively under *Striga*-infested environments. Similarly, the first five high yielding hybrids under *Striga*infested environments (TZEI 127 x TZEI 449, TZdEI 216 x TZEI 402, TZdEI 272 x TZdEI
124, TZEI 461 x TZEI 127 and TZdEI 216 x TZdEI 215) were ranked as the 12th, 68th, 47th, 45th, and 87th, respectively under optimal environments. The presence of differential ranking of genotypes across different environments has been reported for most multienvironment trials in West and Central Africa (Badu-Apraku *et al*. 2008; 2015; Ifie *et al.*,
2015).

As reported earlier in Chapter 5, the presence of highly significant GEI for grain yield under the multiple stress and non-stress environments indicated differential response of the hybrids and the need to identify high-yielding and stable hybrids across the test

environments (Moghaddam and Pourdad, 2009). The GGE biplot identified the hybrids TZEI 127 x TZEI 449 as the most adapted hybrids to the *Striga*-infested environments, while TZEI 376 x TZdEI 69 was the most adapted to the *Striga*-free environments. Ideally, maize genotypes selected for broad adaptation should be both high yielding and highly stable to the target environments (Badu-Apraku *et al.*, 2011b), therefore, the hybrids TZdEI 124 x TZEI 378 and TZdEI 272 x TZdEI 124 were identified as the ideal hybrids for production across the *Striga*-infested and *Striga*-free environments. The hybrids TZdEI 124 x TZdEI 283 and TZdEI 216 x TZdEI 272 were identified as the ideal hybrids for both the low-N and high-N environments. The hybrids TZdEI 215 x TZdEI 192, TZEI 378 x TZdEI 215 and TZEI 3A x TZdEI 192 were the ideal hybrids for production across the optimal, *Striga*-infested and low-N environments. They will therefore be desirable in the savanna zones of WCA where *Striga* infestation and low-N mostly occur simultaneously on farmers' fields.

The ten test environments used in this study were classified into three main groups as follows: Group 1 comprised KWD-HN-16, KWD-LN-17, KWD-LN-16, MOK-NSTR-16, and KWD-HN-17 with TZEI 376 x TZdEI 69 as the best hybrid; Group 2 consisted of MOK-STR-16, NYK-NSTR-17 and NYK-STR-17 with TZEI 127 x TZEI 449 as the best hybrid; while Group 3 was composed of MAN-STR-16 and NYK-STR-16 with TZdEI 192 x TZdEI 216 as the best hybrid. Thus, the grouping of the test environments into distinct groups implied that environments in one group cannot be used to select genotypes for environments in the other group. Thus, the low-N and high-N environments cannot be used to select *Striga* tolerant hybrids and vice versa. This results further confirmed the need for the extensive testing of the set of hybrids in contrasting environments before any

recommendations could be made. Furthermore, the classification of the high-N environments, KWD-HN-16 and KWD-HN-17, and low-N environments, KWD-LN-16 and KWD-LN-17 into one group implied that the contrast between those test environments was not enough, to have possibly caused significant genotype x nitrogen interactions among them. Therefore, they became replicates of each other (Gallais and Coque, 2005). For meaningful cultivar evaluation, the right test environments should be used in variety evaluations (Yan *et al.*, 2010). The environments KWD-HN-16, MAN-STR-16, KWDLN-16 and NYK-NSTR-17 were the most discriminating among the ten test environments, and so provided more useful information about the hybrids, while KWD-LN-17, NYKSTR-17 and NYK-STR-16 were the least discriminating and can be avoided as test environments. In this study, the most discriminating environments were highly correlated with the less discriminating ones. Since correlated environments provide similar information on test genotypes, it is evident that KWD-LN-17, NYK-STR-17 and NYKSTR-16 were redundant and could be dropped to reduce the costs of field evaluation without any loss of information. The test environment KWD-HN-16 was both highly discriminating of the hybrids and most representative of the target environments, it is therefore considered as the ideal environment for selecting superior hybrids (Yan & Rajcan, 2002). The environments KWD-HN-17 and MAN-STR-16 were highly

discriminating of the hybrids, but were not representative of the target environments. Therefore, they may not be appropriate for selecting superior genotypes. However, they could be used in culling unstable hybrids (Badu-Apraku *et al.*, 2011b).

CHAPTER EIGHT

8.1 General discussion

Maize production in savanna zones of WCA is greatly constrained by drought, low soil fertility, and *Striga* infestation (Badu-Apraku *et al.*, 2003). Under field conditions, there are often complex interactions among these stresses with more devastating effects on yield of maize (Cechin & Press 1994; Kim & Adetimirin 1997). In order to improve maize yields, each variety targeted to the savanna zones must be able to withstand a wide range of drought stress and nitrogen availability, and *Striga* infestation, a need that justifies the development and deployment of multiple stress tolerant maize varieties in savanna zones of West and Central Africa.

A series of experiments involving 100 early maturing white and yellow inbred lines from IITA were conducted to identify superior inbred lines based on the performance of multiple traits under optimal growing conditions, low-N and *Striga*-infested environments for the development of hybrids with combined tolerance to *Striga* and low-N, and for population improvement. Information on genetic diversity and population structure is very important in any breeding program for the improvement of traits of interest and the development of outstanding products for commercialization. Using SSR and SNP markers, substantial genetic variability were found among the 100 early maturing maize inbred lines used in the present study. This makes the set of inbred lines unique with the potential to contribute new alleles to breeding programs. The inbred lines were related by pedigree, selection history and endosperm colour, and were grouped into three populations by the SNP markers. They exhibited low heterozygosity within sub-populations and moderate

divergence among sub-populations, suggesting that they could be either directly utilized in hybrid breeding or serve as the gene pool for development of conventional hybrids for Ghana and other countries in WCA. Field testing of the selected set of inbred lines under optimal growing conditions, *Striga*-infested and low-N environments also revealed significantly high genetic variation among the inbred lines for grain yield, days anthesis and silking, ears per plant, ear aspect, plant and ear heights under optimal growing conditions; grain yield, ears per plant, ear aspect, plant height and *Striga* damage syndrome ratings at 8 and 10 WAP under artificial *Striga* infestation; grain yield, days to anthesis, days to silking, ears per plant, ear aspect, ear height and stay green characteristic under low-N environments; and for days to anthesis, days to silking, plant height, ear aspect, ear height and ears per plant across the three research environments. The existence of genetic variability among the inbred lines for those traits indicated that they could serve as parents for the development of productive hybrids for optimal, *Striga* endemic and lowN environments. This result also implied that the inbred lines would contribute favourable alleles for the improvement of tropical breeding populations for *Striga* resistance and lowN tolerance. The significant differences detected for environment and GEI mean squares for grain yield and most other measured traits of the inbred lines under each and across the environments indicated that the environments were diverse and that the expression of most of the traits would not be consistent in the varying test environments (Badu-Apraku *et al*. (2012; 2013) and Akaogu *et al*. (2012). This indicated the need to select for genotypes that had superior performance and stability across the three research environments.

Grain yield is a quantitative trait highly influenced by the environment and controlled by polygenes. Therefore, identification of genotypes with improved grain yields for marginal

production environments is enhanced when screening is based on yield and associated secondary traits under the target environments (Bänziger and Lafitte, 1997; Bänziger *et al.*, 1999). An important objective of this study was to identify reliable secondary traits that could be used to select for grain yield under *Striga*-infested and low-N environments. Path coefficient analysis, and Genotype by Trait (GT) and Trait Association by Environment (ABE) biplot analyses were used for more comprehensive studies of the pattern of association among grain yield and agronomic traits of the selected inbred lines under the target environments. Under optimal growing conditions, path analysis identified days to silking, days to anthesis, ears per plot and anthesis-silking interval as traits with the highest direct effects on grain yield. Conversely, the GT biplot analysis identified ears per plant, ear aspect, plant height, ears and plants per plot as traits with the highest influence on grain yield. Under *Striga*-infested environments, both path and GT biplot analyses identified ear aspect, plant height and days to silking as the most important explanatory traits of grain yield, while GT biplot also picked ears and plants per plot as additional important traits for selection for improved grain yield of the inbred lines under *Striga*-infested environments. Traits such as number of emerged *Striga* plants at 8 and 10 WAP and *Striga* damage syndrome rating at 8 and 10 WAP were not reliable traits for selecting *Striga* resistant inbred lines with high grain yield. Similarly, Badu-Apraku *et al.* (2014) identified ear aspect as the only trait with significant direct effect on yield under artificial *Striga* infestation. Also, Badu-Apraku and Fakorede (2017) reported ears per plant and *Striga* damage at 8 and 10 WAP and ear aspect as the most reliable traits for selecting *Striga*resistant genotypes from the IITA early maturing maize germplasm. The authors also

found number of emerged *Striga* plants to be unreliable for selecting *Striga*-resistant genotypes.

The results of this study are consistent with the findings of Badu-Apraku *et al.* (2014) and Badu-Apraku and Fakorede (2017), and also supported the call for the exclusion of the number of emerged *Striga* plants from the IITA base index for selecting for improved grain yield of early maturing maize under *Striga* infestation, and instead support the call for the inclusion of ear aspect, plant height and days to silking in the base index for selecting *Striga* resistant genotypes.

Days to silking and days to anthesis were identified by both GT biplot and path analyses as reliable traits for selecting low-N tolerant and high yielding inbred lines, while ears per plant, and plant height, ear aspect, ears and plants per plot were identified separately by path and GT biplot analyses, respectively, as traits with high influence on grain yield in low-N environments. Traits such as anthesis-silking interval, stay green characteristic and plant aspect which have been used in the IITA base index for selecting low-N tolerant early genotypes (Lafitte and Edmeades, 1994; Meseka *et al*., 2006) were not among the traits associated with increased grain yield in the present study. Although the use of anthesissilking interval, stay green characteristic and plant aspect for selecting low-N tolerant genotypes has been very successful in the past, there is possible loss of association between these traits and grain yield due to continuous selection for anthesis-silking interval, stay green characteristic and plant aspect in the IITA maize breeding program (Chapman &

Edmeades 1999; Monneveux *et al.,* 2006; 2008; Edmeades *et al.,* 1999, Monneveux *et al.,* 2006). The observed weak associations between grain yield and ASI and stay green characteristic, and strong association between grain yield and days to anthesis, days to

silking and plant height under low-N, implies the need for inclusion of days to anthesis, days to silking and plant height in the IITA base index for the selection of improved grain yield under low-N environments. Furthermore, the ABE biplot analysis identified days to anthesis, days to silking, plants and ears per plot as reliable traits for indirect selection for high grain yield across optimal, *Striga*-infested and low-N environments. This result implied that there is the possibility of using these cheap, easy and fast to measure traits to select inbred lines with combined tolerance to *Striga* and low-N. This conclusion implies a cheaper way to accomplish the development of multiple-stress tolerant hybrids for multistress environments. Using the IITA base index for selecting low-N tolerant genotypes, the inbred lines TZEI 449, TZEI 365, TZEI 485, TZEI 468, TZdEI 238, TZEI 471, TZdEI 283,

TZdEI 272, TZEI 3B, TZEI 472, TZEI 18, TZEI 470, TZdEI 100, TZEI 378, TZEI 13, TZEI 344 and TZEI 475 were characterized as low-N tolerant. Using the IITA base index for selecting *Striga*-tolerant/resistant genotypes, the inbred lines TZEI 485, TZEI 146,

TZEI 16, TZEI 456, TZEI 127, TZEI 13, TZEI 461, TZEI 365, TZEI 136, TZEI 25, TZEI 472, TZdEI 216, TZdEI 215, TZEI 468 and TZEI 157 were characterized as *Striga* tolerant. Based on the multi-stress selection index proposed by Badu-Apraku *et al*. (2016), the inbred lines TZEI 127, TZdEI 283, and TZEI 146. TZEI 485, TZEI 344, TZEI 35, TZEI 124, TZEI 376, TZEI 13, TZdEI 272, TZdEI 215, TZdEI 216, TZEI 379, TZEI 10, TZEI 365, TZEI 25 TZEI 56, TZdEI 69, TZEI 136 and TZEI 157 were identified to possess multiple-stress tolerance to *Striga* infestation and low-N environments.

In plant breeding, the main purpose of trait selection is to improve the trait, by increasing the frequency of desirable genes controlling the trait in the target environments. However,

the selection theory for each trait is dependent on the gene action controlling its inheritance (Beckett and Ludwick, 1979). Therefore, for better understanding of the underlying gene action controlling the inheritance of desired traits of the inbred lines used in the present study, genetic analysis of a subset of 30 of the inbred lines with varying responses to *Striga* parasitism and low-N stress was conducted. The results of the study revealed significant

GCAm, GCAf and SCA effects for grain yield and the other measured traits under optimal, *Striga*-infested, low-N and across environments. The results of this study suggested that both additive and non-additive gene actions were important for the inheritance of grain yield and other measured traits under each environment and across research environments. This result is consistent with the findings of Badu-Apraku *et al*, **(**2015). However, it is inconsistent with the findings of Ifie *et al.* (2015) who reported non-significant SCA effect for the number of emerged *Striga* plants under *Striga*-infested environments and for stay green characteristic under low-N environments. Although, both additive and non-additive gene actions were important in the inheritance of the traits in this study under the target environments, the preponderance of GCA sum of squares over SCA sum of squares for days to silking, days to anthesis, ear height and plant height under optimal growing conditions indicated that additive gene action largely controlled the inheritance of those traits in the hybrids. Musila *et al.* (2010) also found additive gene action to be more important than non-additive gene action in the inheritance of days to anthesis in early maturing inbred lines in optimal environments. The preponderance of GCA over SCA sum of squares for grain yield, plant height and stalk lodging under low-N environments and for grain yield, days to anthesis, days to silking, plant height and ear height across research environments, indicated that additive gene action was the most important gene action that

controlled the inheritance of those traits under the respective test environments. Similarly, the importance of additive gene action over non-additive gene effects in the inheritance of grain yield under low-N was reported by Rizzi *et al.* (1993); Below *et al.* (1997) and Kling *et al.* 1997). However, the present results disagree with the findings of Betran *et al*. (2003b) who found non-additive gene action to be more important in the inheritance of grain yield under low-N. This result implied that early generation testing may be more effective for days to silking, days to anthesis, ear height and plant height under optimal growing conditions, as well as for grain yield, plant height and stalk lodging under low-N environments and for grain yield, days to anthesis and silking, plant height and ear height across environments. This result also imply that promising hybrids can be identified and selected mainly based on the prediction from GCA effects (Baker, 1978; Badu-Apraku *et al*., 2015). However, since SCA effects of the inbred lines were also significant, prediction of hybrid performance based solely on GCA effects of the parents would not be reliable. Furthermore, the preponderance of additive gene action indicates the existence of great potential for the improvement of the traits for optimal and low-N environments through recurrent selection methods (Badu- Apraku *et al.* 2011b). The inheritance of grain yield and other traits under *Striga*-infested environments were controlled by non-additive gene action. Badu-Apraku *et al.* (2015) also found out that the inheritance of grain yield and most other traits under *Striga* infestation is controlled by non-additive gene action. The inheritance of *Striga* emergence count at 8 and 10 WAP was also found to be controlled by non-additive gene action by Kim (1994). On the contrary, Gethi and Smith (2004), Yallou *et al.* (2009), Badu-Apraku and Oyekunle (2012) and Ifie *et al.* (2015) reported that additive gene action is more important in the inheritance of *Striga* damage syndrome rating

and number of emerged *Striga* plants at 8 and 10 WAP in early maturing maize inbreds. The inheritance of plant aspect, ear aspect, ears per plant, stay green characteristic, days to silking and anthesis–silking interval under low-N environments were also controlled by non-additive gene action. The inheritance of stalk lodging, husk cover, plant aspect, ear aspect and ears per plant across research environments were also controlled by nonadditive gene action. Traits controlled by non-additive gene action has the highest magnitude of expression of hybrid vigour (Mulualem and Abate, 2016). Therefore, hybrid development could be employed to exploit heterosis to improve grain yield and the other traits for *Striga* resistance and low-N tolerance (Menkir and Akintunde, 2001).

The significance of GCAm x E and GCAf x E interactions for grain yield and most of the other traits under optimal, low-N and *Striga*-infested environments and across environments indicated that the GCA effects of the inbred lines when used as a male or female parent would vary in the contrasting environments. This result is consistent with the findings of Annor and Badu-Apraku (2016) for grain yield and other traits of extraearly QPM inbred lines under optimal and low-N environments and across both environments. The larger sum of squares of GCAf compared to the GCAm observed for grain yield and the other traits under each and across environments indicated that maternal inheritance played a more important role in the inheritance of grain yield and the other traits under the respective environments. This result implied a possible role of cytoplasmic gene effects on grain yield and its components under each and across the research environments. Derera *et al.* (2008) reported a modification in grain yield due to maternal effects under drought/low-N, anthesis-silking interval and ear aspect under well-watered environments in maize hybrids. Oyekunle and Badu-Apraku (2014) found that the inheritance of grain yield under

optimal conditions is controlled by maternal effects. On the other hand, anthesis–silking interval, plant aspect, husk cover and ears per plant under low-N, and number of emerged *Striga* plants at 8 and 10 WAP, days to silking, ears per plant and days to anthesis under *Striga*-infested environments were found to be controlled by paternal effects. It is important to note that the differences in the mode of inheritance of traits reported in this study may have been influenced by the germplasm type and the level of stress intensity imposed in this study.

Under optimal environments, the inbreds TZdEI 40, TZdEI 124, TZEI 127, TZdEI 192, TZdEI 215 and TZEI 449 had significant and positive GCAf effects for grain yield while TZEI 8, TZdEI 40 and TZEI 127 displayed significant positive GCAm effects for grain yield. This result suggested that these inbred lines could contribute favourable genes to improve grain yield in their progenies when used as female and male parents, respectively. Under *Striga* infestation, TZdEI 124 and TZEI 127, and TZdEI 40, TZEI 127, TZdEI 216, TZEI 470 would contribute favorable alleles to improve the yield potentials of their progenies when used as female and male parents, respectively. The inbred lines TZEI 127, TZdEI 192, TZdEI 216, TZEI 298 and TZEI 402 had significant and negative effects for both GCA_m and GCA_f for *Striga* damage syndrome ratings and number of emerged *Striga* plants at 8 and 10 WAP. The negative GCA effects of these inbred lines for those traits indicated that they would contribute favourable alleles to reduce *Striga* damage and the number of emerged *Striga* plants in their progenies when used either as female or male parent. Such inbred lines would be very useful in multiple trait selection programs for grain yield as reduced *Striga* damage syndrome is a good indicator for improved yield under *Striga*-infested environments (Badu-Apraku *et al.,* 2015).The negative and significant

GCAm and GCAf effects of stay green characteristic of TZdEI 192, TZEI 127, TZdEI 272, and TZEI 485 suggested that they would contribute genes that would delay leaf senescence in their progenies when used either as male or female parents. The inbred lines TZdEI 124 and TZdEI 215 obtained significant positive GCAm effects for grain yield and so they would contribute favorable genes for yield improvement when used as a male parent. The inbred lines TZdEI 69, TZEI 8 and TZEI 365 when used as female parent would contribute alleles to delay leaf senescence in their progenies when used only as a female parent. Therefore, TZdEI 192, TZEI 127, TZdEI 272, TZEI 485, TZdEI 124, TZdEI 215, TZdEI 69, TZEI 8 and TZEI 365 would be useful in recurrent selection programs for delayed leaf senescence and improved yield under low-N environments. The significance of GCA effects for days to anthesis, days to silking, plant aspect, ear aspect and ears per plant of TZdEI 40, TZdEI 124, TZEI 127 and TZdEI 215 across research environments makes them invaluable parents for the development of outstanding hybrids with multiple tolerance to *Striga* infestation and low-N environments. They would also be invaluable sources of desirable alleles for improvement of *Striga and* low-N tolerance in population improvement programs.

Classification of inbred lines into appropriate heterotic groups is essential to maximize their potential usefulness for the development of productive hybrids and synthetics as well as for creation of new heterotic groups (Badu-Apraku *et al.*, 2015). The HGCAMT heterotic grouping method clustered the 30 inbred lines used in the genetic studies into three heterotic groups each under low-N, optimal growing conditions and across research environments and four heterotic groups under *Striga*-infested environments. The SSR-GD and SNP-GD methods clustered the 30 inbred lines into seven and five heterotic groups,

respectively. In the present study, the breeding efficiency of the SNP-GD heterotic grouping method was the highest under *Striga*-infested, low-N environments and across the three research environments, while the HGCAMT had the highest breeding efficiency under optimal environment. Therefore, the SNP-GD method was identified as the most efficient heterotic grouping method followed by the HGCAMT method, while the SSRGD was the least efficient in grouping the inbred lines under each and across the three research environments. Similarly, Badu-Apraku *et al*. (2015a, b) reported superiority of SNP-GD method over HGCAMT method in heterotic groupings of early maturing inbred lines. Badu-Apraku *et al*., (2013) also found the HGCAMT method to be more efficient than the SSR-GD method in the heterotic groupings of early maturing inbred lines. The superior performance of the SNP-GD method compared to the HGCAMT in grouping the inbred lines into heterotic groups suggested that SNP markers can be used to group inbred lines in the IITA maize program that are yet to be field tested in hybrid combinations. This result is consistent with reports by Badu-Apraku *et al.,* (2013a) and Akinwale *et al.,* (2014). Furthermore, since the SNP-GD was the most efficient heterotic grouping method in the present study, selection of inbred lines for the development of heterotic hybrids should be from opposite groups formed by the SNP-GD method. Additionally, inbred lines within each of the five clusters formed by the SNP-GD method could be recombined to form heterotic populations that could be improved through recurrent selection for grain yield and *Striga* and low-N tolerance to serve breeding programs and seed companies in WCA.

The exploitation of heterosis in hybrid development is primarily based on the identification of diverse parents and their cross combinations capable of producing the highest level of transgressive segregates (Dhoot *et al*., 2017). The magnitude of both mid-parent and

better-parent heterosis observed in this study were very low for most traits under low-N and optimal environments. The moderate to high magnitude of mid-parent and betterparent heterosis expressed by the hybrids under *Striga*-infested environments could be attributed to the relatively large SCA effects over GCA effects of most of the parental lines under *Striga*-infested environments (Mulualem and Abate, 2016). Most of the hybrids expressed non-significant heterosis for most of the traits measured in this study. The significant positive mid-parent and better-parent heterosis for days to anthesis and silking exhibited by TZdEI 215 x TZdEI 238 under optimal environments indicated a significant delay in the flowering of the hybrids as compared to the earliness in flowering of both parents. The hybrid TZEI 472 x TZEI 470 also exhibited significantly higher number of days to silking than the average number of days taken by both parents to silk. The expression of lateness in flowering by TZdEI 215 x TZdEI 238 and TZEI 472 x TZEI 470 under optimal conditions may not be desirable as the target of this study is to develop early maturing varieties, otherwise lateness in flowering will probably not have any adverse effects on grain yield under optimal conditions (Sharifi and Namvar, 2016)). Under low-N environments, TZEI 298 x TZEI 365 produced significantly more ears per plant than the average number of ears per plant produced by both parents and even by the parent with the highest number of ears per plant. This makes TZEI 298 x TZEI 365 a very desirable cross, and would be very useful under low-N environments since increased number of ears per plant is a good indicator of improved yield under nitrogen stress (Bänziger *et al.*, 2000). The hybrid TZdEI 272 x TZdEI 124 expressed significant negative mid-parent and betterparent heterosis for stay green characteristic, which showed that it had delayed leaf senescence under low-N environments when compared to its parents under the same

environments. The expression of prolonged leaf longevity under low-N is very desirable as delayed senescence is a key component of nitrogen use efficiency in maize (Bänziger *et al*., 2000). The only significant positive mid-parent and better-parent heterosis recorded in this study was expressed by the hybrid TZEI 127 x TZEI 449 under *Striga*-infested environment. It produced 83.02% more grains over the average grain yield of both parents and 73.06% more grain over the better-parent under *Striga*-infested environments. Therefore, TZEI 127 x TZEI 449 would be very desirable in *Striga* endemic *areas.* All 150 hybrids tested in this study showed significant mid-parent and better-parent heterosis for anthesis-silking interval under *Striga*-infested environments. This result suggested improved synchronization of male and female flowering of the hybrids resulting in relatively shorter days from anthesis to silking than the average days taken by both parent and even for the better parent to silk after anthesis. The reduction in anthesis-silking interval for almost all the hybrids under *Striga*-infested environments is striking, since reduction in anthesis-silking interval of maize under stress is a good indication of stress tolerance and improved grain yield (Singh and Sarkar, 1991 and Subramanyam, 1992; Badu-Apraku and Fakorede, 2017). About 76% and 98% of the hybrids expressed significant positive mid-parent and better-parent heterosis for the number of emerged *Striga* plants at 8 and 10 WAP, respectively. This indicated that many hybrids supported higher number of emerged *Striga* plants than their parents. The marked increase in the number of emerged *Striga* plants per se does suggest that the hybrids are more susceptible to *Striga*; it could also be interpreted that the hybrids are more tolerant to *Striga* as they produced higher yield than the parental inbreds. However, hybrids should be further tested

to confirm the superior performance in terms of grain yield and other *Striga* adaptive traits before any recommendation for commercialization is made.

A prime objective of the present study was to identify the most stable and high-yielding hybrids for commercialization in SSA. The significant mean square observed among the single-cross hybrids for grain yield under optimal, low-N and *Striga*-infested environments and across environments indicated that adequate genetic variability existed among the hybrids to allow good progress from selection under the contrasting environments. This finding is consistent with the results of Badu-Apraku *et al.* (2011a) and Badu-Apraku and Oyekunle (2012). The presence of significant environmental mean square for grain yield under optimal, low-N and *Striga*-infested environments and across environments was a demonstration of the uniqueness and variability of the environments and emphasized the need for multi-location testing for several years for each of the contrasting environments (Badu-Apraku *et al.*, 2016). The mean grain yield of the hybrids under optimal conditions was 2496 kg ha^{-1}. The average yield reduction due to N stress was 46.7%, while yield reduction due to *Striga* parasitism was 51.76%. The magnitude of yield reduction due to stress is indicative of whether the severity of the stress was high enough to reveal genetic differences among the hybrids for a particular stress. According to Gallais and Coque (2015), for maximum expression of specific genetic variability for low N input, it would be better to evaluate genotypes with sufficient stress leading to yield reduction of about 35-40%. This confirms that the relative yield reduction of 46.7% recorded under low-N environments in this study was severe and adequate to easily discriminate among the hybrids for nitrogen stress tolerance. Reports by Badu-Apraku and Fakorede (2017) have demonstrated that a yield reduction of 35-56% between *Striga*-infested and non-infested

plots is adequate to separate *Striga* resistant genotypes from non-tolerant ones. It is therefore apparent that the 56.7% yield reduction observed in the present study was severe enough to reveal adequate separation of the hybrids for *Striga* tolerance. The high magnitude of yield reduction in *Striga*-infested and low-N environments also implied that the correlation between the performance of the hybrids under stress and non-stress environments is very low. Therefore, selection under optimal conditions for performance under stress environments would not be effective (Bänziger *et al*. 1997; Presterl *et al*. (2003). This justified the need for screening the hybrids under optimal, *Striga*-infested and low-N environments before any selection was done. Moreover, the presence of highly significant GEI for grain yield across the test environments indicated differential responses of the hybrids across the test environments. Therefore, the need to select high yielding hybrids with stable performance across research environments cannot be overemphasized. (Moghaddam and Pourdad, 2009). Ideally, maize genotypes selected for broad adaptation such as those desired in the three northern regions of Ghana should be both high yielding and highly stable across drought, low-N and *Striga*-infestation. The GGE biplot identified the hybrid TZEI 127 x TZEI 449 as the most adapted hybrid under *Striga*-infested environments, while TZEI 376 x TZdEI 69 was identified as the most adapted hybrid under Striga-free environments. The hybrids TZdEI 124 x TZEI 378 and TZdEI 272 x TZdEI 124 were the ideal hybrids across *Striga*-infested and *Striga*-free environments. The hybrids TZdEI 124 x TZdEI 283 and TZdEI 216 x TZdEI 272 were also the ideal hybrids for both low-N and high-N environments. The hybrids TZdEI 215 x TZdEI 192, TZEI 378 x TZdEI 215 and TZEI 3A x TZdEI 192 had high stable yields across optimal, *Striga*infested and low-N environments. They will therefore be desirable in the savanna

zones of Ghana and other countries in West and Central Africa where *Striga* infestation and low-N mostly occurs simultaneously on farmers' fields.

CHAPTER NINE

9.1 Conclusions and Recommendations

9.1.1 Conclusion

The major findings and implications of the study may be summarized as follows:

1. Substantial genetic variability existed among the 100 early maturing white and yellow inbred lines used in this study, making them unique with the potential to contribute new alleles to tropical breeding programs. The inbred lines were related by pedigree, selection history and endosperm colour.

2. Although SSR markers used in this study were highly informative, the use of large number of SNP markers did not only make it comparable with the SSR for genetic diversity analysis, but it also performed better than SSR in cluster and population structure analyses.

3. The relative performance of the inbred lines in grain yield and agronomic traits were altered by *Striga* parasitism and low-N stresses. The grain yield of the inbred lines were reduced by 22% and 36% under low-N and *Striga*-infested environments, respectively when compared to their yield under optimal growing conditions.

4. Generally, high yielding inbred lines with stress tolerance were late maturing. Under *Striga*-infested environments, high grain yield was associated with good ear aspect, shorter plants and large number of ears per plot. High yielding inbred lines in low-N environments had prolonged days to silking and anthesis, more ears per plant, taller plants and good ear aspect, whereas inbred lines with high grain yield across optimal, *Striga-infested* and lowN

environments had prolonged days to silking and anthesis, larger number of plants and ears per plot.

5. Anthesis-silking interval and stay green characteristic had very weak associations with grain yield under low-N, implying that they were unreliable traits for indirect selection for high grain yield under low-N environments. Similarly, the number of emerged *Striga* plants and *Striga* damage syndrome ratings at 8 and 10 WAP also had weak associations with grain yield, and are therefore not reliable traits for indirect selection for *Striga* resistant inbred lines.

6. There were significant differences among the hybrids and test environments for grain yield and most measured traits under optimal, *Striga*-infested and low-N environments and across environments, indicating that the test environments were unique and diverse and that adequate genetic variability existed among the hybrids to allow effective selection and improvement of the measured traits.

7. General combining ability (GCAf and GCAm) and SCA sum of squares were significant for grain yield and other measured traits under optimal, *Striga*-infested and low-N environments and across environments, indicating that both additive and non-additive gene actions were important in the inheritance of most traits of the hybrids.

8. The inheritance of grain yield under low-N environments and across the three research environments were largely controlled by additive gene action, while the inheritance of grain yield under optimal and *Striga*-infested environments were largely controlled by nonadditive gene action. Except for *Striga* damage syndrome rating at 8 WAP, the

inheritance of all traits studied under *Striga*-infested environments were largely controlled by nonadditive gene action.

9. The inbred lines TZdEI 124 and TZEI 127, and TZdEI 40, TZEI 127, TZdEI 216, TZEI 470 had significant positive GCAf and GCAm for grain yield under *Striga*-infested environments. The inbred lines TZEI 127, TZdEI 192, TZdEI 216, TZEI 298 and TZEI 402 were superior with significant and negative GCA_m and GCA_f effects for both *Striga* damage syndrome ratings and number of emerged *Striga* plants at 8 and 10 WAP. These inbred lines could be utilized as either male or female parents to develop high yielding *Striga* resistant/tolerant hybrids.

10. The inbreds TZdEI 192, TZEI 127, TZdEI 272, and TZEI 485 were superior with significant negative GCAm and GCAf effects for stay green characteristic under low-N environments. Also, TZdEI 124 and TZdEI 215 showed significant positive GCAm effects for grain yield under low-N environments. These inbred lines could therefore be used to develop hybrids with delayed leaf senescence and high grain yield for low-N environments. Moreover, TZdEI 40, TZdEI 124, TZEI 127 and TZdEI 215 obtained desirable GCA effects for days to anthesis, days to silking, plant aspect, ear aspect and ears per plant across the three research environments. They would contribute favourable genes for use in population improvement programs for multiple stress tolerance to *Striga* infestation and low-N environments.

11. The SNP-GD heterotic grouping method was superior to HGCAMT and SSR-GD method in grouping the inbred lines under *Striga*-infested, low-N and across the three research environments, while the HGCAMT method was superior to the other two methods under

optimal environment. Therefore, the SNP-GD was identified as the best heterotic grouping method in the present study.

12. The mid-parent and better parent heterosis expressed by the hybrids were very low for most measured traits under low-N and optimal environments and across environments. Large number of the hybrids expressed non-significant heterosis for most of the traits measured under each and across environments. The hybrid TZdEI 272 x TZdEI 124 exhibited significant mid-parent and better-parent heterosis for grain yield under *Striga*-infested environments. Therefore, TZdEI 272 x TZdEI 124 could be further evaluated and exploited for commercial production in *Striga* endemic areas. Under low-N, TZEI 298 x TZEI 365 and TZdEI 272 x TZdEI 124 showed desirable significant heterosis for ears per plot and stay green characteristic, respectively, and thus they could be used in low-N population improvement programs or for hybrid development.

13. The hybrids TZdEI 215 x TZdEI 192, TZEI 378 x TZdEI 215 and TZEI 3A x TZdEI 192 were identified as high yielding and most stable across optimal, *Striga*-infested and low-N environments. They possess multiple stress tolerance to *Striga* and low-N and therefore are the ideal hybrids for the savanna zones of Ghana and other countries in WCA.

9.1.2 Recommendations

1. The inbred lines exhibited high levels of genetic variability for grain yield and agronomic traits desirable for *Striga* resistance and low-N tolerance. Therefore, the inbred lines with superior performance under *Striga*-infested and/or low-N environments could be used by plant breeders as sources of resistance/tolerance genes for the development of

multiplestress tolerant hybrids, synthetic varieties and populations in maize breeding programs.

2. It is recommended that breeders and other users of the IITA multiple-trait base index for early maturing low-N tolerant genotypes replace anthesis-silking interval and stay green characteristic in the index with days to anthesis, days to silking and plant height. Ear aspect should also be included in the base index for selecting *Striga* resistant/tolerant inbred lines.

3. For maximum heterotic effects, selection of inbred lines for development of *Striga* resistant/tolerant and low-N tolerant hybrids and synthesis should be guided by the heterotic groups formed by the SNP-GD heterotic grouping method.

4. A relatively larger number of SNP markers were more efficient at detecting the genetic diversity among the inbred line than SSR markers, and also more efficient at heterotic groupings of the inbred lines than HGCAMT and SSR-GD methods. Therefore, SNP markers are recommended for the genetic diversity and heterotic groupings of IITA inbred lines that are yet to be field tested in hybrid combinations. However, since most breeding programs in WCA are poorly resourced, the practical used of SNP markers would rely on the affordability of the SNP technology and the availability of resources to adequately maintain the relatively large heterotic groups revealed by the SNP markers.
5. Given that the majority of the hybrids in the present study expressed very low and nonsignificant heterosis for grain yield and most measured traits under the three research environments, it is recommended that plant breeders employ early generation testing and recurrent selection methods to select and improve the set of inbred lines used in the present study.

6. The hybrids TZdEI 215 x TZdEI 192, TZEI 378 x TZdEI 215 and TZEI 3A x TZdEI 192 combined high yields with multiple-tolerance to *Striga* and low-N. With an average yield advantage of 19% over the yields of the local checks under optimal environments, and 47% and 37% yield advantages over the local checks under *Striga*-infested and low-N environments, they are recommended for extensive testing in multi-location trials and for eventual release and commercialization in the savanna zones of West and Central Africa by researchers and other actors in the maize value-chain.

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APPENDICES

Appendix 1 List of polymorphic simple sequence repeat markers and their corresponding annealing temperatures

Primer name	Forward Sequence	Reverse sequence	Annealing temp (°C)
NC130	GCACATGAAGATCCTGCTGA	TGTGGATGACGGTGATGC	59
NC133	AATCAAACACACACCTTGCG	GCAAGGGAATAAGGTGACGA	58
PHI008	CGGCTACGGAGGCGGTG	GATGGGCCCACACATCAGTC	65
PHI015	GCAACGTACCGTACCTTTCCGA	ACGCTGCATTCAATTACCGGGAAG	64
PHI034	TAGCGACAGGATGGCCTCTTCT	GGGGAGCACGCCTTCGTTCT	65
PHI046	ATCTCGCGAACGTGTGCAGATTCT	TCGATCTTTCCCGGAACTCTGAC	64
PHI053	AACCCAACGTACTCCGGCAG	CTGCCTCTCAGATTCAGAGATTGAC	64
PHI059	AAGCTAATTAAGGCCGGTCATCCC	TCCGTGTACTCGGCGGACTC	64
PHI070	GCTGAGCGATCAGTTCATCCAG	CCATGGCAGGGTCTCTCAAG	64
PHI072	ACCGTGCATGATTAATTTCTCCAGCCTT	GACAGCGCGCAAATGGATTGAACT	64
PHI084	AGAAGGAATCCGATCCATCCAAGC	CACCCGTACTTGAGGAAAACCC	64
PHI087	GAGAGGAGGTGTTGTTTGACACAC	ACAACCGGACAAGTCAGCAGATTG	64
PHI108411	CGTCCCTTGGATTTCGAC	CGTACGGGACCTGTCAACAA	60
PHI109188	AAGCTCAGAAGCCGGAGC	GGTCATCAAGCTCTCTGATCG	61
PHI109275	CGGTTCATGCTAGCTCTGC	GTTGTGGCTGTGGTGGTG	61
PHI109642	CTCTCTTTCCTTCCGACTTTCC	GAGCGAGCGAGAGAGATCG	63
PHI112	TGCCCTGCAGGTTCACATTGAGT	AGGAGTACGCTTGGATGCTCTTC	64
PHI233376	CCGGCAGTCGATTACTCC	CGAGACCAAGAGAACCCTCA	61
PHI328175	GGGAAGTGCTCCTTGCAG	CGGTAGGTGAACGCGGTA	61
PHI331888	TTGCGCAAGTTTGTAGCTG	ACTGAACCGCATGCCAAC	58
PHI374118	TACCCGGACATGGTTGAGC	TGAAGGGTGTCCTTCCGAT	60
PHI420701	GATGTTTCAAAACCACCCAGA	ATGGCACGAATAGCAACAGG	69
PHI423796	CACTACTCGATCTGAACCACCA	CGCTCTGTGAATTTGCTAGCTC	59
PHI448880	CGATCCGGAGGAGTTCCTTA	CCATGAACATGCCAATGC	59
PHI452693	CAAGTGCTCCGAGATCTTCCA	CGCGAACATATTCAGAAGTTTG	60
PHI453121	ACCTTGCCTGTCCTTCTTTCT	CAAGCAAGACTTTTGATCAGCC	60
UMC1061	AGCAGGAGTACCCATGAAAGTCC	TATCACAGCACGAAGCGATAGATG	63
UMC1136	CTGCATACAGACATCCAACCAAAG	CTCTCGTCTCATCACCTTTCCCT	63
UMC1143	CGTGGTGGGATGCTATCCTTT	GACACTAGCAATGTTCAAAACCCC	62
UMC1196	CGTGCTACTACTGCTACAAAGCGA	AGTCGTTCGTGTCTTCCGAAACT	63
UMC1279	CAATCCAATCCGTTGCAGGTC	GATGAGCTTGACGACGCCTG	63

Appendix

2 Summary of clustering and population structure of the 94 inbred lines genotyped with 15,047 SNP markers

Sr. No.	Inbred lines	Endosperm colour	SNP NJ cluster	SNP structure
1	TZdEI 215	white	C3	Admixture
2	TZdEI 69	white	C3	Admixture
3	TZdEI 84	white	C3	Admixture
4	TZdEI 94	white	C3	3
5	TZdEI 72	white	C3	Admixture
6	TZdEI 280	white	C3	3
7	TZdEI 153	white	C3	3
8	TZdEI 139	white	C3	Admixture
9	TZdEI 131	white	C3	3
10	TZdEI 120	white	C3	3
11	TZdEI 221	white	C3	3
12	TZdEI 222	white	C3	3
13	TZdEI 216	white	C3	Admixture
14	TZdEI 283	white	C3	3
15	TZdEI 92	white	C3	Admixture
16	TZdEI 157	white	C3	Admixture
17	TZdEI 100	white	C3	3
18	TZdEI 275	white	C3	3
19	TZdEI 260	white	C3	Admixture
20	TZdEI 238	white	C3	3
21	TZdEI 227	white	C3	3
22	TZdEI 124	white	C3	3
23	TZdEI 82	white	C3	3
24	TZdEI 71	white	C3	Admixture
25	TZEI 295	white	C3	3
26	TZEI 298	white	C3	3
27	TZEI 323	white	C3	3
28	TZEI 344	white	C3	3
29	TZEI 3A	white	C3	3
30	TZEI 3B	white	C3	3
31	TZEI 376	white	C3	3
32	TZEI 378	white	C3	3
33	TZEI 379	white	C3	3
34	TZEI 402	white	C3	3
35	TZEI 413	white	C3	3
36	TZEI 7	white	C3	3
37	TZEI 18	white	C3	3
38	TZEI 31	white	C3	3
39	TZEI 56	white	C3	3
40	TZEI 19	white	C3	3
41	TZEI 83	white	C3	3
42	TZEI 5	white	C3	Admixture
43	TZEI 26	white	C3	Admixture
44	TZEI 35	white	C3	Admixture
45	TZdE I24	Yellow	C1	1

46	TZEI 8	yellow	C2	Admixture
47	TZEI 9	yellow	C2	Admixture
48	TZEI 10	yellow	C2	Admixture

2 Cont'd

Sr. No.	Inbred lines	Endosperm colour	SNP NJ cluster	SNP structure
49	TZEI 127	yellow	C2	Admixture
50	TZdEI 192	white	C3	Admixture
51	TZEI 471	yellow	C2	2
52	TZEI 468	yellow	C2	2
53	TZEI 461	yellow	C2	2
54	TZEI 467	yellow	C2	2
55	TZEI 449	yellow	C2	2
56	TZEI 464	yellow	C2	2
57	TZEI 146	yellow	C2	Admixture
58	TZEI 17	yellow	C2	Admixture
59	TZEI 129	yellow	C3	3
60	TZEI 23	yellow	C2	Admixture
61	TZEI 462	yellow	C2	2
62	TZEI 460	yellow	C2	2
63	TZEI 456	yellow	C2	2
64	TZEI 135	yellow	C3	3
65	TZEI 124	yellow	C2	Admixture
66	TZEI 25	yellow	C2	Admixture
67	TZEI 157	yellow	C2	Admixture
68	TZEI 16	yellow	C2	Admixture
69	TZEI 13	yellow	C2	2
70	TZEI 136	yellow	C2	Admixture
71	TZdEI 52	yellow	C1	Admixture
72	TZdEI 65	Yellow	C1	1
73	TZdEI 68	Yellow	C1	1
74	TZdEI 40	yellow	C1	Admixture
75	TZdEI 41	Yellow	C1	1
76	TZdEI 42	Yellow	C1	1
77	TZdEI 12	yellow	C1	Admixture
78	TZdEI 16	yellow	C1	Admixture
79	TZdEI 17	Yellow	C1	1
80	TZdEI 46	Yellow	C1	1
81	TZdEI 21	Yellow	C1	1
82	TZdEI 37	yellow	C1	Admixture
83	TZdEI 48	yellow	C1	Admixture
84	TZEI 520	yellow	C2	2
85	TZEI 497	yellow	C2	2
86	TZEI 485	yellow	C2	Admixture
87	TZEI 476	yellow	C2	2
88	TZEI 474	yellow	C2	2
89	TZEI 475	yellow	C2	2
90	TZEI 472	yellow	C2	2
91	TZEI 470	yellow	C2	2

92	TZEI 465	yellow	C2	2
93	TZEI 448	yellow	C2	2
94	TZEI 365	white	C3	3

3 Initial soil properties of experimental field used for the Low-N experiments

Soil properties	Soil depth		Interpretation	
	0-15 cm	15-30 cm	High	Low
pH (1:1)	7.38	6.98	>6.5	<5.8
Organic C (%)	1.32	0.58	>10.0	<4.0
Total N (%)	0.16	0.1	>0.5	<0.2
Ex Ca (Cmolc/kg)	6	3.94	>10.0	<4.0
Ex Mg (Cmolc/kg)	5.18	3.1	>4.0	<0.5
Ex K (Cmolc/kg)	0.25	0.2	>0.6	<0.2
Ex Na (Cmolc/kg)	0.21	0.2	>1.0	<1.0
Av P (Mg/kg)	35.82	12.13	>50.0	<15.0

Ex: Exchangeable, Av: Available

Appendix 4 Grain yield and multiple-trait base index value of the 100 inbred lines evaluated under optimal growing conditions, *Striga*-infested and low-N environments

Entry	Grain yield (t ha^{-1})				LD	STRRAT1	STRRAT2	Base index		
	Optmal	Low-N	*Striga*	Across env				Low-N	*Striga*	Across Env
TZDEI 100	681	835	832	783	5	5	7	2.8	-0.1	-3.8
TZDEI 12	1369	524	566	820	5	5	6	-7.5	1.5	-0.9
TZDEI 120	556	423	508	496	6	6	7	-3.5	-1.6	-5.5
TZDEI 124	859	485	662	669	6	4	6	-5.8	3.5	-2.4
TZDEI 131	872	747	511	710	5	5	6	1.7	-1.6	-1.9
TZDEI 139	397	661	448	502	5	5	6	-3.7	-0.7	-3.0
TZDEI 153	881	762	524	722	5	6	6	-2.2	-1.3	-2.6
TZDEI 157	420	382	360	387	5	5	5	2.7	-1.9	-1.6
TZDEI 16	447	299	411	386	7	6	5	-12.8	-2.5	-8.1
TZDEI 17	764	451	614	610	4	6	6	-0.3	-0.7	-1.2
TZDEI 192	780	823	727	777	4	6	6	-3.2	2.1	1.2
TZDEI 21	427	488	206	374	5	5	5	-2.1	-5.4	-6.9
TZDEI 213	1371	981	617	990	5	5	6	-3.6	0.2	0.8
TZDEI 215	1332	806	617	918	4	5	5	0.3	1.7	4.6
TZDEI 216	931	628	635	731	5	5	5	2.5	5.0	4.5
TZDEI 221	992	643	699	778	5	6	6	-5.3	1.0	-1.7
TZDEI 222	521	1311	431	754	4	6	6	-1.6	-2.1	-0.7
TZDEI 227	1033	713	346	697	5	5	5	-2.8	-1.7	1.3
TZDEI 228	1063	677	576	772	6	5	6	-4.8	-0.1	-4.4
TZDEI 233	1205	643	861	903	5	6	7	-6.2	2.5	0.9
TZDEI 238	698	827	550	692	4	5	6	9.5	1.7	2.0
TZDEI 24	1271	773	832	959	5	6	7	-1.6	4.6	2.3
TZDEI 260	674	418	809	634	6	5	5	-9.8	1.3	-5.5
TZDEI 272	1373	744	536	884	5	4	5	4.2	0.1	4.6
TZDEI 275	1135	663	336	711	4	6	7	-5.0	-5.5	-2.6
TZDEI 280	323	555	595	491	6	6	6	-12.4	-0.9	-6.9
TZDEI 283	1836	1406	538	1260	4	4	5	8.8	0.7	9.1
TZDEI 37	790	705	643	713	5	4	4	-3.0	1.3	-1.5
TZDEI 40	1224	729	919	957	5	5	6	3.7	4.5	1.3
TZDEI 41	689	501	504	565	5	5	5	-5.8	0.2	-2.8
TZDEI 42	743	540	613	632	6	6	7	-5.0	-2.2	-8.0
TZDEI 46	935	705	305	648	5	5	5	-8.1	-3.3	-1.7
TZDEI 48	1327	632	519	826	5	6	7	-6.3	-3.6	-3.6
TZDEI 51	782	556	1173	837	6	7	6	-7.6	1.4	-10.4
TZDEI 52	943	621	883	816	6	5	6	-2.7	1.8	-2.6
TZDEI 65	890	396	562	616	6	6	5	-11.1	-1.1	-8.2
TZDEI 68	586	319	411	439	6	4	5	-4.7	-0.1	-1.7
TZDEI 69	1083	1235	700	1006	5	5	7	5.6	1.3	3.6
TZDEI 71	462	443	417	441	5	5	5	-0.4	-0.6	-3.6
TZDEI 72	1400	520	353	758	5	4	4	-1.7	1.2	3.4
TZDEI 82	1052	583	673	769	5	5	5	0.5	-0.4	2.0
TZDEI 84	1673	543	243	820	5	5	5	-3.9	-6.0	0.3
TZDEI 92	529	455	584	523	4	4	4	-12.6	-2.6	-2.9
TZDEI 94	536	398	294	409	6	5	5	0.8	-5.0	-6.3
TZEI 10	1139	1213	406	919	5	4	4	3.2	-0.9	4.1
TZEI 124	2021	763	300	1028	5	4	4	-4.4	-1.3	5.4
TZEI 127	1826	795	1073	1231	4	5	5	-3.3	7.6	9.5
TZEI 129	1022	679	328	676	5	5	5	-1.1	-2.2	-0.2
TZEI 13	954	1367	981	1101	5	5	5	10.8	4.3	5.0

Grand mean	1076	741	581	768	5	5	6			

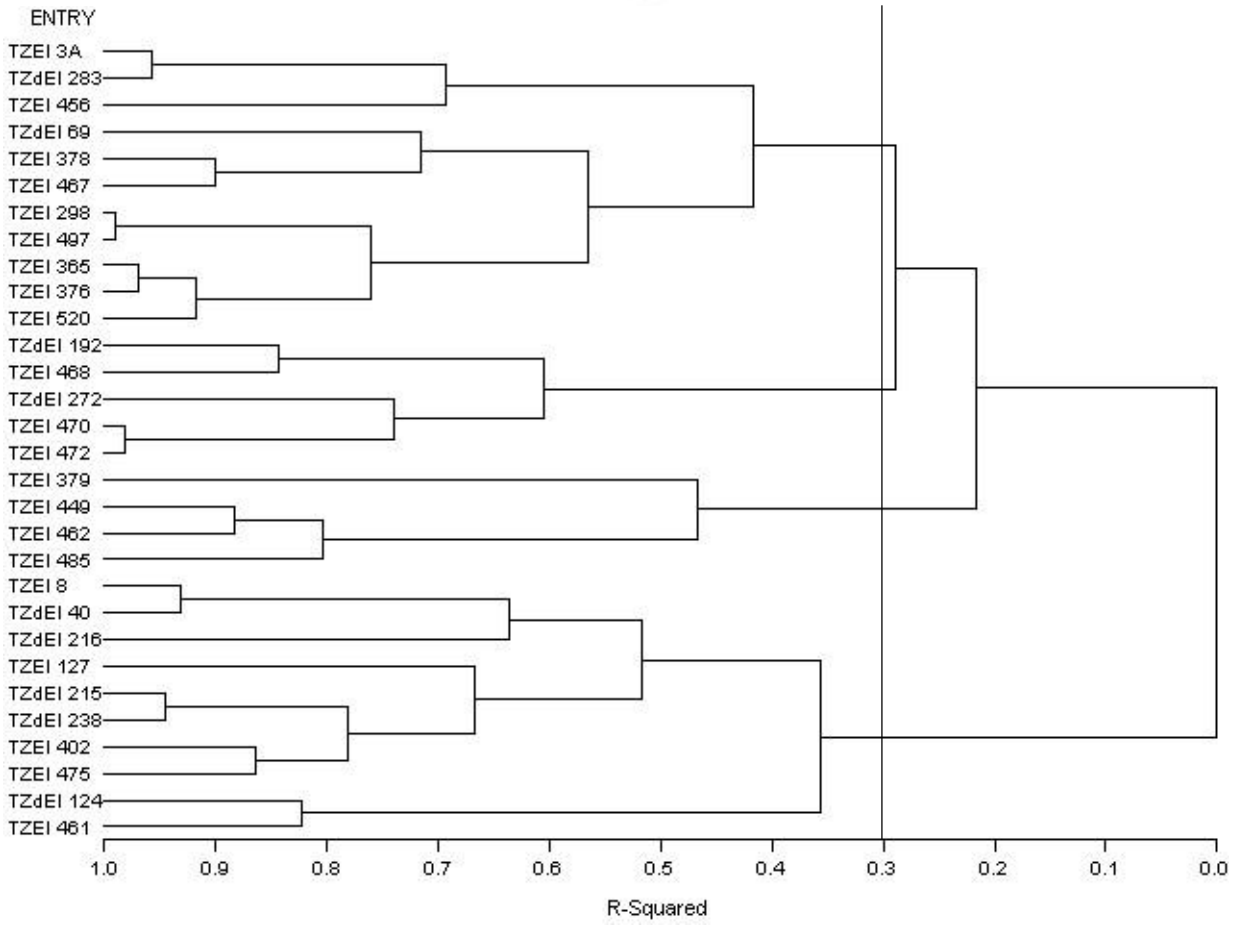
LD=Leaf death score, STRRAT1=*Striga* damage syndrome rating at 8WAP, STRRAT2= *Striga* damage syndrome rating at 8WAP, Env=Environment

Appendix 4 Cont'd

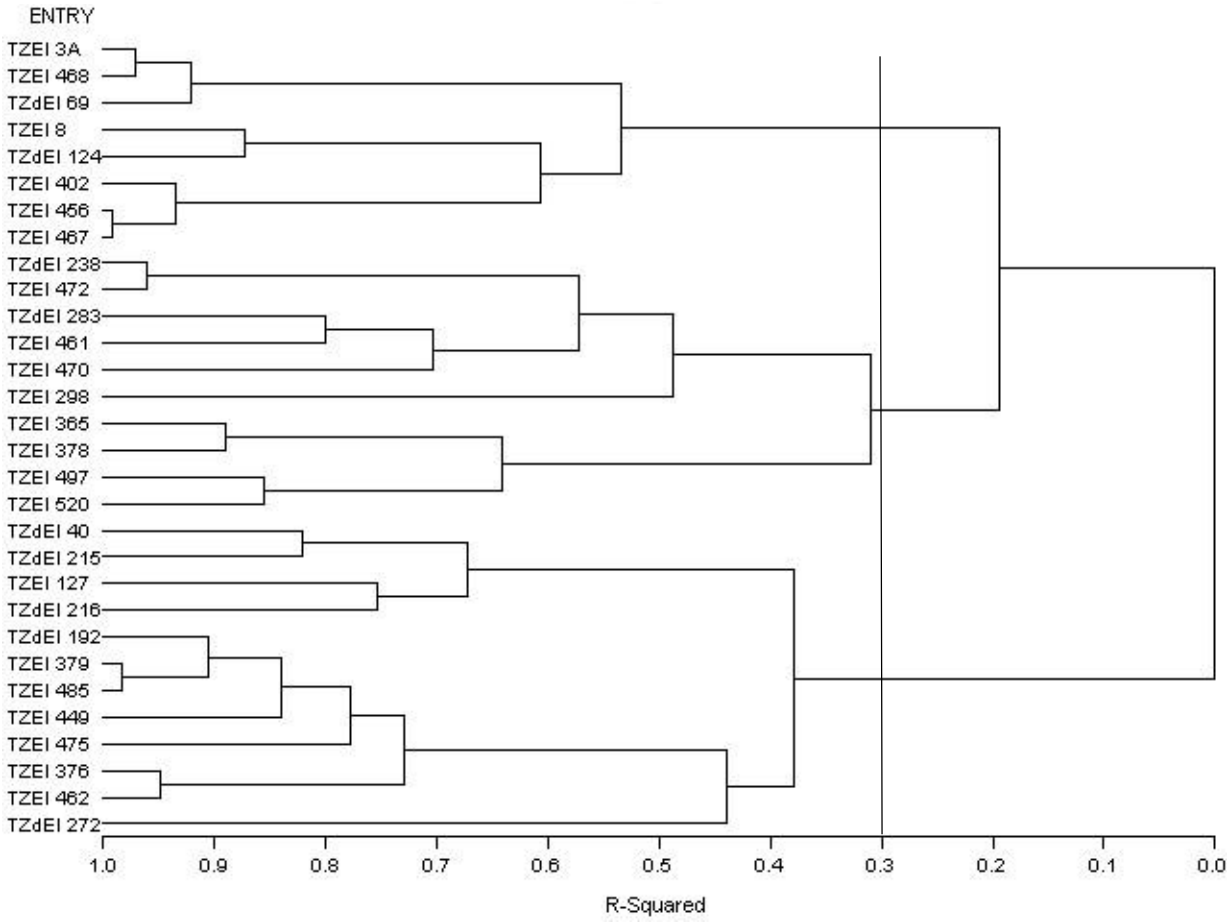
Entry	Grain yield ha^{-1})				LD	STRRAT1	STRRAT2	Base index		
	Optmal	Low-N	*Striga*	Across env				Low-N	*Striga*	Across Env
TZEI 135	1009	739	628	792	5	5	5	-1.4	1.2	0.8
TZEI 136	930	566	784	760	5	4	5	-0.9	3.1	3.5
TZEI 146	2253	327	651	1077	5	3	3	-2.6	2.6	7.9
TZEI 157	633	689	595	639	4	4	5	-1.6	2.8	3.4
TZEI 16	1321	399	636	785	4	4	4	-3.7	3.9	3.5
TZEI 17	822	681	419	641	5	5	7	-3.0	-3.0	-6.3
TZEI 18	1993	820	607	1140	5	5	6	3.8	-1.2	2.9
TZEI 19	1427	569	512	836	4	6	6	-2.4	-0.6	0.2
TZEI 23	1241	1251	358	950	6	6	8	4.1	-4.3	-1.9
TZEI 25	1357	567	731	885	4	5	5	-2.8	2.4	4.1
TZEI 26	1448	1036	435	973	5	6	6	0.2	-3.7	-0.2
TZEI 295	1134	882	511	842	6	7	7	2.2	-3.2	-3.9
TZEI 298	1288	627	768	894	5	6	6	-1.6	0.8	2.4
TZEI 31	1687	1095	359	1047	5	6	6	-4.3	-8.0	-6.4
TZEI 323	560	476	424	487	5	5	6	8.8	-2.0	-4.1
TZEI 344	2105	1004	555	1221	5	5	5	5.0	1.1	6.8
TZEI 35	1957	1648	525	1377	4	5	5	7.8	-4.2	5.6
TZEI 365	544	865	824	744	4	5	5	2.9	4.0	4.3
TZEI 376	1105	731	379	738	4	4	4	5.3	-0.2	5.1
TZEI 378	808	854	685	782	5	6	7	5.9	-0.2	-2.7
TZEI 379	1551	1308	641	1167	5	7	6	4.8	0.3	4.6
TZEI 3A	535	716	522	591	5	5	6	-0.3	1.5	-2.0
TZEI 3B	1238	997	570	935	5	6	6	4.7	-1.6	-0.2
TZEI 402	942	723	580	748	5	4	4	2.5	0.5	1.2
TZEI 413	2322	855	516	1231	5	6	6	0.2	-1.0	2.2
TZEI 443	1086	1065	621	924	5	5	5	-0.5	1.2	2.1
TZEI 448	1291	693	440	808	4	4	6	3.9	-0.9	-1.0
TZEI 449	970	1173	292	812	4	5	6	7.7	-2.7	3.4
TZEI 456	873	699	582	718	5	4	4	2.9	1.3	0.2
TZEI 460	809	959	577	782	5	4	4	2.7	1.3	-0.5
TZEI 461	685	589	872	715	4	4	5	1.6	5.0	3.1
TZEI 462	1172	586	509	756	4	6	6	1.5	-1.6	0.2
TZEI 464	953	766	574	764	5	6	6	0.9	0.2	-0.4
TZEI 465	643	634	550	609	4	4	4	-0.7	-3.8	-3.0
TZEI 467	804	718	791	771	5	6	7	2.3	2.1	-1.3
TZEI 468	893	898	779	857	4	5	5	10.4	2.5	0.3
TZEI 470	554	931	867	784	5	6	6	3.6	2.3	0.0
TZEI 471	915	793	461	723	4	6	7	6.9	-2.3	-2.4
TZEI 472	794	1000	664	819	5	4	5	4.2	2.4	1.2
TZEI 474	1205	933	561	900	3	4	5	-0.5	-0.7	2.7
TZEI 475	1328	1045	560	978	5	5	5	4.0	0.6	2.9
TZEI 476	2198	1101	433	1244	5	5	5	2.6	-2.8	1.5
TZEI 485	1531	758	764	1018	4	3	3	11.4	4.4	6.6
TZEI 497	543	686	830	686	5	6	6	1.0	3.7	-1.8
TZEI 5	1636	454	722	937	5	7	7	0.2	-0.5	-2.2
TZEI 520	1928	636	622	1062	5	5	6	4.9	1.1	1.6

TZEI 56	1876	802	722	1133	6	5	6	-0.3	2.0	4.0
TZEI 7	1068	765	478	770	4	5	5	2.3	-0.4	2.5
TZEI 8	1159	739	545	814	5	6	6	17.0	1.6	-0.5
TZEI 83	785	488	428	567	5	5	6	-3.0	-0.9	-2.8
TZEI 9	866	408	439	571	5	4	4	-2.0	-0.2	-0.3
Grand mean	1076	741	581	768	5	5	6			

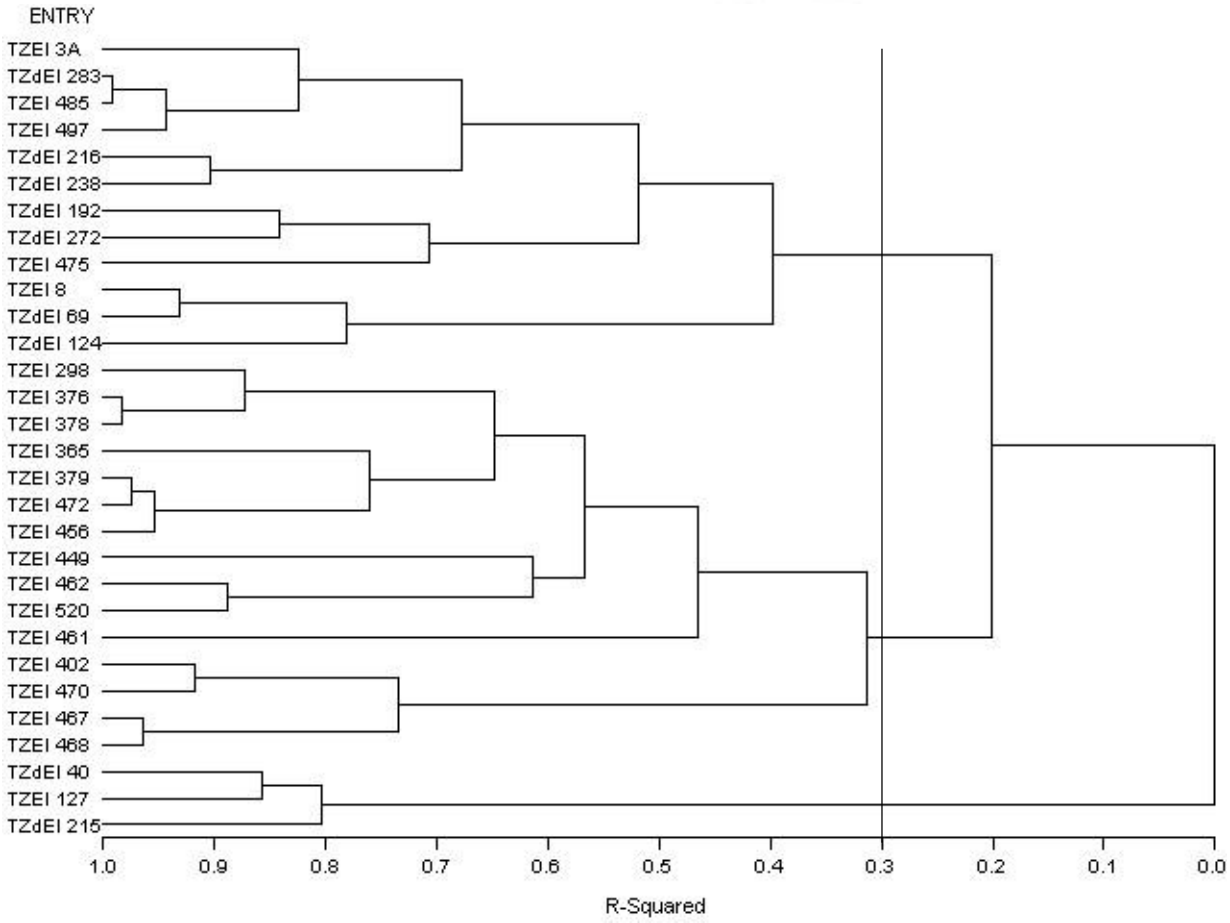
LD=Leaf death score, STRRAT1=*Striga* damage syndrome rating at 8WAP, STRRAT2= *Striga* damage syndrome rating at 8WAP, Env=Environment



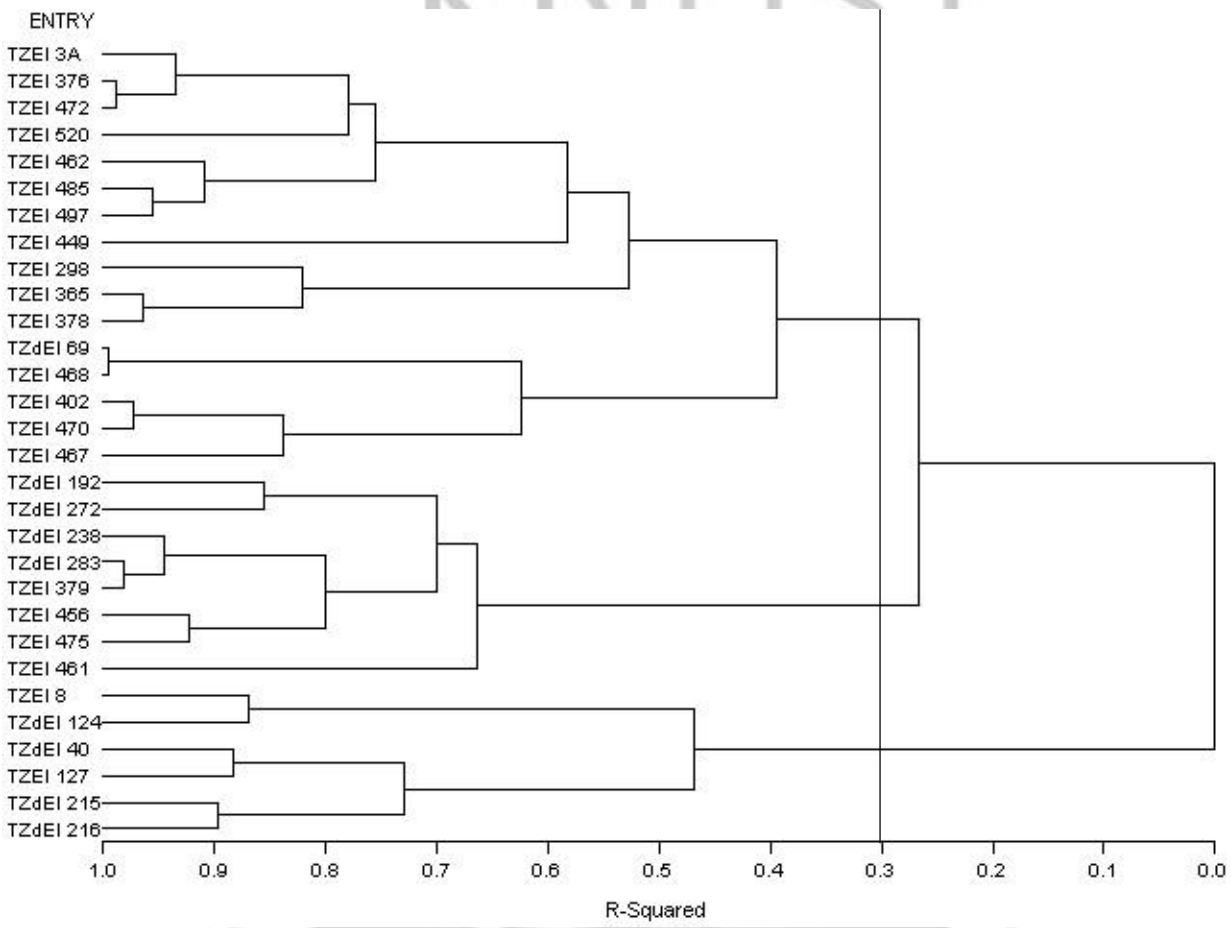
Appendix 5 Dendrogram of 30 early maturing maize inbred lines constructed from HGCAMT effects method using Ward's minimum variance cluster analysis across four environments under *Striga* infested conditions, 2016-2017



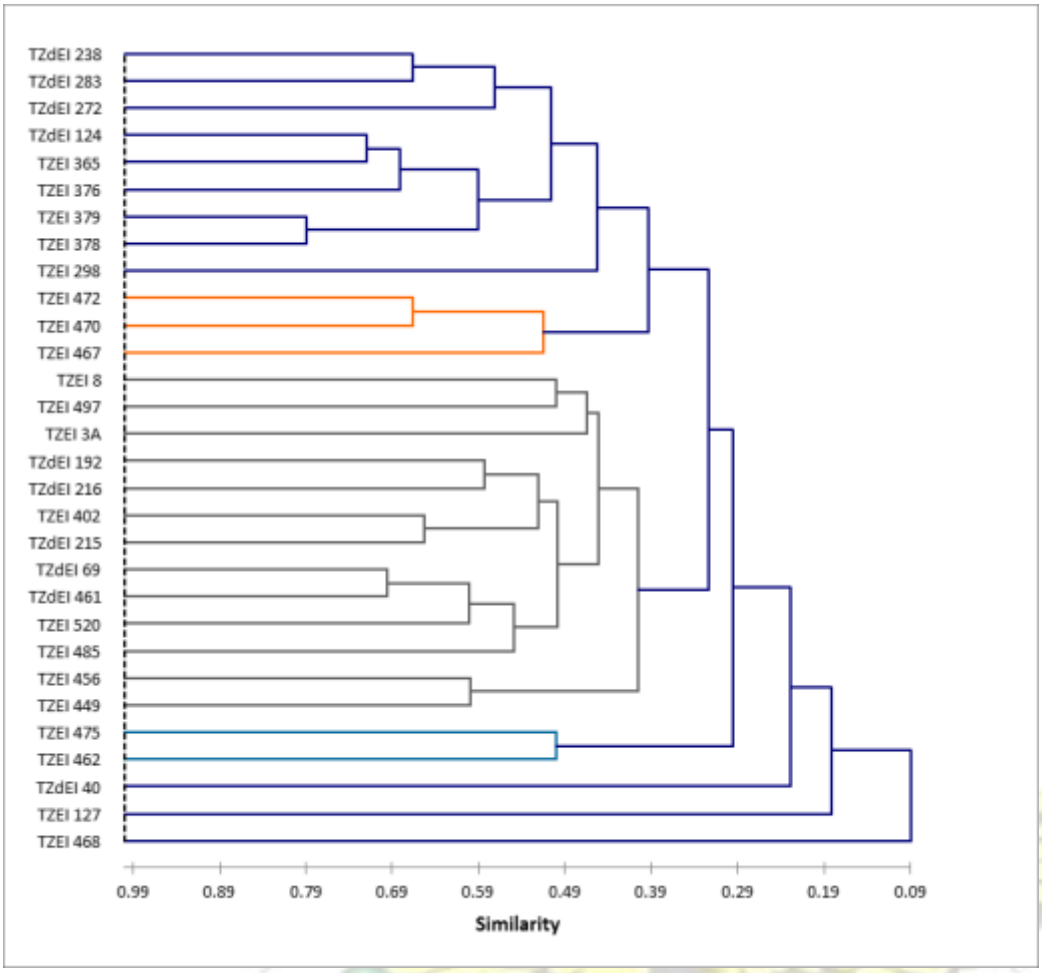
Appendix 6 Dendrogram of 30 early maturing maize inbred lines constructed from HGCAMT effects method using Ward's minimum variance cluster analysis across two environments under low-N growing conditions, 2016-2017



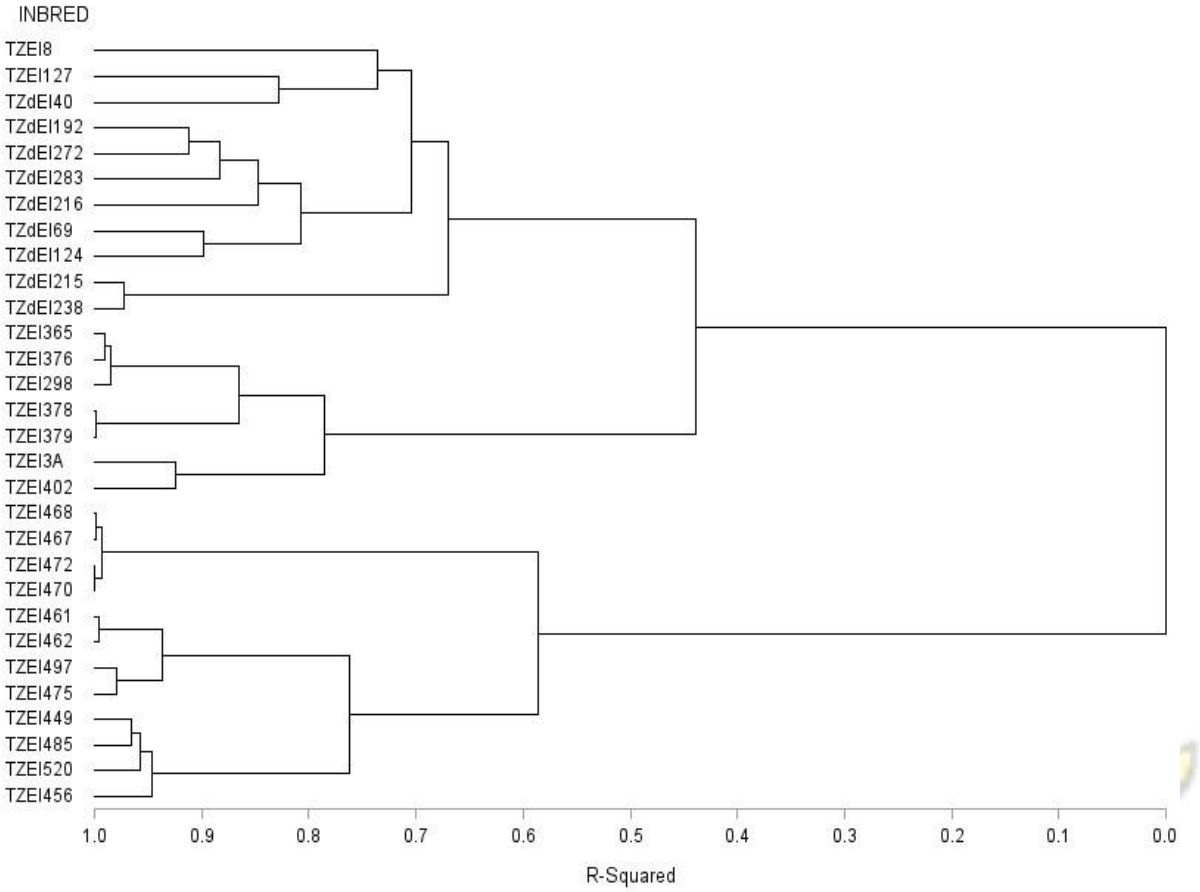
Appendix 7 Dendrogram of 30 early maturing maize inbred lines constructed from HGCAMT effects method using Ward's minimum variance cluster analysis across four environments under optimal growing conditions, 2016-2017



Appendix 8 Dendrogram of 30 early maturing maize inbred lines constructed from HGCAMT effects method using Ward's minimum variance cluster analysis across 10 research environments under *Striga*-infested, low-N and optimum growing conditions, 2016-2017



Appendix 9 Dendrogram of 30 early maturing maize inbred lines constructed using UPGMA clustering method based on 15 SSR markers



Appendix 10 Dendrogram of 30 early maturing maize inbred lines constructed using Ward's minimum variance clustering method based on 15,047 SNP markers

Appendix

11 Mid-parent and Better-parent heterosis for some agronomic traits of hybrids with significant heterosis estimates under optimal and low-N environments

	Days to anthesis		Days to silking		Plant height		Ear height	
Pedigree	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
Optimal environment								
TZdEI 215 x TZdEI 238	5.24*	4.70	6.23*	5.71*	2.00	1.00	7.90	6.80
TZEI 472 x TZEI 470	5.70	5.00	6.08*	5.20	-10.70	-11.4	-14.4	-14.90
low-N environment								
TZdEI 216 x TZEI 298	-2.00	-3.58	-2.76	-4.23	-5.68	-9.93	-8.91	-15.80
TZdEI 283 x TZEI 298	2.13	1.28	0.58	-0.24	15.65	12.11	18.03	11.49
TZEI 462 x TZEI 8	1.26	-1.09	1.50	-0.65	13.02	11.37	17.89	17.66
TZEI 461 x TZEI 462	0.84	0.83	0.75	0.34	-9.35	-10.20	-16.67	-18.19
TZEI 298 x TZEI 365	5.41	5.11	6.99	6.57	-6.92	-9.36	-1.79	-3.24
TZEI 379 x TZEI 298	-0.88	-2.00	-1.05	-2.24	2.43	2.43	3.66	-0.93
TZdEI 272 x TZdEI 124	-0.13	-0.79	7.29	6.00	3.98	1.55	-12.80	-15.06
TZEI 470 x TZEI 520	-2.99	-5.68	-2.69	-5.31	-2.34	-5.86	-3.07	-4.85
TZEI 3A x TZdEI 124	-3.58	-4.22	-5.41	-6.01	-6.98	-10.69	-14.64	-14.99
TZEI 497 x TZEI 520	6.72*	6.12	8.36*	7.78	-21.90*	-25.31*	-23.51*	-28.91*
TZEI 456 x TZEI 449	-2.30	-2.77	-4.21	-5.06	17.69	13.50	26.05*	20.42
TZEI 468 x TZEI 467	5.43	5.40	5.01	4.59	-20.27*	-20.40	-18.63	-20.84

MPH, Mid-parent heterosis; BPH, Better-parent heterosis

Appendix 12

Appendix 11 Cont'd

Pedigree	Root lodging		Stalk lodging		Ears per plant		Stay green	
	MPH	BPH	MPH	BPH	MPH	BPH	MPH	BPH
Optimal environment								
TZdEI 215 x TZdEI 238	-11.9	-12.30	6.40	3.20	-8.70	-16.70		
TZEI 472 x TZEI 470	7.20	5.60	26.10	22.00	-23.4	-27.20		
Low-N environment								
TZdEI 216 x TZEI 298	-20.92	-37.71*	-10.34	-24.93	-5.69	-5.91	1.51	-0.49
TZdEI 283 x TZEI 298	69.44*	60.19*	58.80*	57.23*	32.68	31.14	4.74	3.21
TZEI 462 x TZEI 8	50.24*	49.48	41.37	38.10	29.65	17.91	-7.79	-8.31
TZEI 461 x TZEI 462	37.41*	26.13	33.14	23.73	21.32	19.85	-9.80	-10.26
TZEI 298 x TZEI 365	63.08*	60.33*	54.72*	51.63*	84.06*	78.53*	4.59	3.29
TZEI 379 x TZEI 298	42.21*	30.02	25.89	16.11	26.86	24.01	8.24	6.94
TZdEI 272 x TZdEI 124	75.51*	74.20*	16.72	16.17	20.27	14.70	-36.40*	-41.50*
TZEI 470 x TZEI 520	34.88	34.42	41.51*	39.13*	-7.97	-14.61	-0.65	-0.87
TZEI 3A x TZdEI 124	-22.64	-29.71	-2.75	-6.15	-8.80	-16.83	20.25*	19.59*
TZEI 497 x TZEI 520	-4.45	-12.65	-9.16	-14.38	-15.38	-16.02	8.19	8.03
TZEI 456 x TZEI 449	11.26	4.80	3.97	-4.60	20.29	18.80	3.86	2.91
TZEI 468 x TZEI 467	14.68	4.72	6.24	0.53	-10.99	-16.77	3.50	1.74

MPH, Mid-parent heterosis; BPH, Better-parent heterosis **Estimates of heterosis for some agronomic traits of the 150 early**

maturing maize hybrids under *Striga*-infested environments

Pedigree	ASI		STRCO1		STRCO2	
	MPH	BPH	MPH	BPH	MPH	BPH
TZdEI 216 x TZEI 3A	-47.37*	-49.82*	58.72	41.29	598.97**	540.38**
TZdEI 124 x TZEI 379	-56.82*	-61.98*	39.43	24.97	352.47**	290.35**
TZEI 470 x TZdEI 40	-51.92*	-55.89*	80.2*	56.24	497.92**	410.98**
TZEI 467 x TZEI 475	-62.68*	-65*	118.29*	105.35*	576.35**	547.3**
TZEI 402 x TZEI 376	-57.73*	-57.92*	96.72*	80.90*	712.41**	629.6**
TZEI 470 x TZEI 461	-61.07*	-61.16*	74.8*	45.31	425.89**	335.5**
TZEI 365 x TZdEI 69	-51.41*	-54.72*	103.74*	89.97*	190.19**	169.26**

TZEI 378 x TZEI 402	-45.83*	-47.79*	14.51	10.75	274.83**	235.07**
TZEI 467 x TZEI 497	-60.04*	-63.21*	331.86**	317.58**	729.48**	688.12**
TZdEI 216 x TZEI 402	-48.59*	-51.11*	37.29	31.95	91.83*	87.71*
TZdEI 69 x TZdEI 272	-43.77*	-48.96*	371.09**	370.75**	1316.31**	1135.88**
TZdEI 215 x TZdEI 238	-51.42*	-53.48*	32.34	26.78	209.26**	200.09**
TZdEI 216 x TZEI 298	-50.53*	-50.92*	110.95*	97.09	448.52**	427.33**
TZdEI 69 x TZEI 402	-59.52*	-64.76*	106.35*	90.59*	614.91**	559.77**
TZEI 298 x TZdEI 124	-52.53*	-53.45*	124.66**	93.94*	413.32**	346.37**
TZEI 8 x TZEI 468	-60.21*	-63.32*	123.08*	91.00*	359.59**	297.87**
TZEI 379 x TZdEI 215	-45.67*	-50.58*	91.27*	82.95	205.07**	203.2**
TZdEI 216 x TZdEI 272	-59.18*	-59.33*	29.25	15.05	176.9*	165.92*
TZdEI 216 x TZdEI 215	-54.15*	-57.8*	43.26	30.64	244.54**	228.33**
TZdEI 272 x TZdEI 238	-56.96*	-62.34*	257.64**	210.28**	349.67**	272.03**
TZEI 520 x TZEI 127	-49.4*	-50.32*	275.15**	256.28**	576**	548.4**
TZEI 378 x TZEI 3A	-52.86*	-55.65*	156.83*	129.95*	514.57**	417.85**
TZEI 472 x TZEI 475	-55.34*	-58.24*	148.26**	133.39*	322.19**	301.84**
TZdEI 40 x TZEI 467	-52.47*	-54*	108.88*	103.69*	435.18**	407.74**
TZEI 462 x TZEI 449	-53.96*	-57.09*	131.98*	109.65*	446.3**	382.27**
TZEI 468 x TZEI 462	-42*	-43.77*	203.22**	201.40**	479.53**	456.95**
TZEI 485 x TZEI 467	-55.36*	-57.09*	418.75**	413.98**	688.68**	664.45**
TZEI 3A x TZdEI 192	-63.97*	-68.27*	200.25**	176.43**	505.93**	435.53**
TZdEI 192 x TZdEI 216	-56.06*	-56.64*	92.32*	76.17	412.83**	357.11**
TZEI 298 x TZdEI 192	-50.29*	-53.05*	-2.10	-4.26	186.39**	168.48**
TZEI 127 x TZEI 449	-57.38*	-60.69*	167.14**	142.53**	547.1**	501.32**
TZdEI 40 x TZEI 462	-59.17*	-59.52*	74.57*	69.67	345.25**	343.18**
TZdEI 40 x TZEI 127	-49.11*	-51.76*	370.71**	358.98**	610.19**	580.89**
TZEI 365 x TZEI 379	-57.97*	-60.73*	183.78**	158.86**	360.27**	320.03**
TZEI 402 x TZdEI 238	-60.99*	-62.16*	223.98**	217.39**	591.13**	559.18**
TZdEI 215 x TZdEI 124	-59.43*	-60.63*	182.00**	179.80**	592.35**	566.8**
TZEI 468 x TZEI 456	-56.44*	-59.45*	203.11**	196.67**	511.38**	497.86**
TZdEI 40 x TZEI 472	-51.92*	-52.53*	80.76*	79.25*	314.63**	287.32**
TZEI 497 x TZEI 461	-54.33*	-55.8*	383.23**	324.40**	724.24**	647.66**
TZEI 456 x TZEI 8	-59.8*	-64.52*	225.34**	225.27**	260.61**	243.87**
TZEI 365 x TZEI 378	-55.78*	-59.23*	319.16**	311.16**	916.28**	865.66**
TZEI 298 x TZdEI 238	-51.19*	-55.4*	93.23*	74.47	533.64**	485.6**
TZdEI 192 x TZdEI 283	-48.84*	-52.27*	99.89*	97.07*	217**	202.02**
TZdEI 40 x TZEI 456	-56.21*	-58.36*	223.14**	205.84**	514.94**	506.88**
TZdEI 238 x TZdEI 283	-58.51*	-61.88*	406.89**	384.65**	682.9**	647.97**
TZEI 462 x TZEI 475	-55.12*	-58.68*	107.66*	94.31*	243**	223.63**
TZEI 127 x TZEI 497	-50.48*	-54.03*	199.23**	169.43**	516.56**	433.25**
TZEI 475 x TZEI 461	-45.5*	-47.68*	280.72**	269.16**	673.72**	643.82**
TZEI 449 x TZEI 468	-51.69*	-52.18*	154.44**	126.74*	324.37**	287.13**

Appendix Cont'd

Pedigree	ASI		STRCO1		STRCO2	
	MPH	BPH	MPH	BPH	MPH	BPH
TZdEI 283 x TZEI 298	-51.41*	-51.71*	73.92	58.98	556.45**	530.12**
TZEI 467 x TZEI 449	-49.82*	-54.08*	166.54**	160.05*	181.42**	173.57**
TZEI 449 x TZEI 520	-45.73*	-48.1*	85.2*	81.94*	155.13**	150.85*
TZdEI 238 x TZdEI 216	-54.48*	-55.81*	32.93	28.84	36.96	33.47
TZdEI 69 x TZdEI 215	-55.77*	-56.28*	163.91**	157.08*	319.81**	297.45**
TZEI 485 x TZEI 127	-62.16*	-64.38*	93.56*	91.80*	497.68**	473.19**
TZEI 467 x TZEI 470	-46.42*	-47.92*	88.13*	82.86*	149.15**	137.48*
TZdEI 283 x TZEI 402	-54.75*	-56.89*	70.89	52.11	251.83**	231.92**
TZEI 461 x TZEI 127	-53.3*	-55.3*	108.54*	91.94*	230.84**	226.66**
TZEI 472 x TZEI 497	-59.19*	-62.32*	88.8*	72.83	247.7**	233.35**
TZEI 456 x TZEI 497	-54.47*	-55.8*	90.12*	88.89*	162.19**	160.14*
TZEI 379 x TZEI 402	-58.57*	-60.12*	157.99**	134.22*	343.79**	329.35**
TZEI 8 x TZEI 485	-51.35*	-52.7*	112.64*	92.51*	187.9**	161.64**
TZEI 462 x TZEI 8	-53.7*	-57.81*	52.77	38.42	285.08**	252.37**
TZEI 461 x TZEI 462	-60.24*	-63.56*	137.56*	119.31*	757.82**	708.9**
TZEI 449 x TZdEI 40	-51.56*	-55.83*	282.25**	270.07**	833.96**	770.3**
TZdEI 283 x TZdEI 272	-50.41*	-50.5*	210.34**	198.25**	287.72**	245.34**
TZEI 449 x TZEI 485	-59.05*	-60.84*	125.29*	112.94**	327.74**	311**
TZdEI 124 x TZEI 378	-54.66*	-55.49*	86.62*	79.60*	232.75**	228.83**
TZdEI 192 x TZEI 379	-48.92*	-50.36*	58.2	52.51	78.87	74.62
TZdEI 272 x TZEI 365	-54.12*	-57.32*	-2.54	-9.14	144.3*	114.31*
TZdEI 238 x TZEI 378	-55.92*	-61.39*	95.82*	91.90*	252.82**	243.26**
TZdEI 124 x TZdEI 283	-50.71*	-52.4*	82.21*	71.17	437.03**	394.35**
TZEI 378 x TZdEI 215	-59.42*	-63.13*	34.99	23.84	320.37**	266.94**
TZEI 298 x TZEI 365	-63.76*	-64.68*	55.36	51.29	362.95**	357.81**
TZEI 379 x TZEI 298	-58.49*	-58.69*	263.12**	238.78**	523.85**	514.39**
TZEI 298 x TZEI 376	-53.38*	-58.38*	147.88*	138.12*	285.44**	279.1**
TZEI 3A x TZEI 376	-61.11*	-62.73*	120.34*	106.35*	359.36**	338.04**
TZEI 376 x TZdEI 69	-55.12*	-56.89*	289.92**	262.52**	1125.52**	1096.72**
TZEI 472 x TZEI 470	-56.37*	-57.46*	74.7*	59.14	337.48**	318.08**
TZEI 468 x TZEI 472	-58.48*	-58.89*	293.84**	283.66**	673.84**	647.87**
TZEI 475 x TZEI 485	-52.54*	-55.99*	253.33**	218.18**	692.46**	612.55**
TZEI 8 x TZdEI 40	-55.28*	-56.27*	326.14**	320.31**	728.97**	718.04**
TZEI 520 x TZEI 472	-61.25*	-64.34*	202.25**	191.80**	565.25**	521.7**
TZEI 379 x TZ dEI 272	-58.3*	-58.68*	-42.51	-43.54	193.37*	167.52*
TZEI 475 x TZEI 520	-55.63*	-56.21*	224.79**	203.37**	644.57**	583.9**
TZEI 497 x TZEI 485	-51.89*	-52.07*	-23.11	-23.31	212.73**	197.83**
TZEI 520 x TZEI 462	-49.94*	-52.99*	212.74**	196.08**	560.77**	557.39**
TZEI 8 x TZEI 520	-53.68*	-58.63*	132.23**	118.13*	450.01**	410.76**
TZEI 468 x TZEI 127	-55.55*	-58.75*	-35.33	-35.93	174.07**	172.12**
TZEI 497 x TZEI 468	-46.88*	-49.54*	-17.64	-22.83	155.67*	131.29*
TZEI 456 x TZEI 449	-58.43*	-59.91*	209.97**	209.14**	882.89**	802.63**
TZEI 456 x TZEI 475	-53.19*	-58.28*	3.78	0.23	127.15*	123.67*
TZEI 461 x TZEI 467	-54.78*	-57.6*	23.97	14.09	282.04**	281.37**
TZEI 8 x TZEI 461	-55.56*	-58.29*	291.65**	277.56**	649.66**	612.52**
TZEI 468 x TZEI 467	-56.65*	-58.95*	93.67*	91.86*	220.53**	214.8**

TZEI 461 x TZEI 472	-51.92*	-56.78*	200.88**	172.65*	360.89**	354.19**
TZEI 449 x TZEI 461	-56.1*	-56.49*	143.81**	124.93*	342.62**	298.18**
TZEI 379 x TZEI 3A	-43.96*	-47.22*	325.84**	318.15**	817.17**	785.19**
TZEI 520 x TZEI 456	-53.65*	-54.66*	103.72*	87.96*	459.78**	452.7**

Pedigree	ASI		STRCO1		STRCO2	
	MPH	BPH	MPH	BPH	MPH	BPH
TZdEI 124 x TZdEI 216	-62.21*	-65.45*	162.6**	159.22**	316.17**	310.56**
TZdEI 215 x TZEI 365	-53.78*	-54.86*	349.03**	299.37**	729.76**	653.5**
TZEI 470 x TZEI 485	-49.27*	-51.18*	147.97*	133.17*	340.54**	316.5**
TZEI 467 x TZEI 8	-59.02*	-61.98*	190.03**	182.15**	634.07**	625.56**
TZEI 456 x TZEI 470	-51.41*	-52.7*	283.57**	283.13**	590.21**	582.52**
TZdEI 192 x TZEI 378	-55.32*	-60.29*	205.9**	194.21**	604.94**	527.4**
TZdEI 238 x TZEI 379	-53.92*	-54.49*	105.77*	87.53*	523.29**	456.46**
TZEI 485 x TZEI 462	-60.07*	-60.69*	84.73*	83.65*	350.57**	313.27**
TZEI 470 x TZEI 468	-48.78*	-49.64*	-8.11	-8.21	273.2**	272.44**
TZEI 461 x TZEI 456	-51.19*	-53.45*	-6.20	-11.14	392.55**	372.44**
TZEI 462 x TZEI 497	-52.24*	-55.2*	58.31	44.27	198.85**	184.01**
TZEI 127 x TZEI 8	-46.92*	-51.14*	292.35**	255.26**	510**	446.5**
TZEI 3A x TZdEI 365	-50.73*	-53.14*	37.00	26.63	226.31**	209.54**
TZEI 472 x TZEI 8	-51.62*	-55.23*	32.18	20.31	216.69**	192.23**
TZdEI 283 x TZdEI 215	-46.28*	-50.64*	225.05**	204.44**	528.27**	508.44**
TZEI 402 x TZEI 365	-52.71*	-56.97*	101.69*	83.1*	267.83**	228.74**
TZEI 402 x TZdEI 124	-47.8*	-52.77*	336.65**	323.52**	644.34**	629.46**
TZdEI 215 x TZEI 376	-60.11*	-62.74*	166.88**	140.35*	361.17**	320.87**
TZdEI 238 x TZdEI 69	-50.72*	-51.46*	133.01**	117.47*	465.52**	436.92**
TZEI 520 x TZEI 467	-47.99*	-50.01*	134.98**	123.18*	227.67**	211**
TZEI 376 x TZEI 378	-53.49*	-58.33*	-8.34	-9.81	152.54**	152.2**
TZEI 365 x TZdEI 283	-60.37*	-61.55*	6.49	1.92	81.41*	77.48**
TZEI 485 x TZEI 472	-47.09*	-47.4*	38.78	35.21	219.89**	215.1**
TZdEI 283 x TZEI 3A	-58.28*	-60.29*	209.09**	197.01**	319.52**	315.48**
TZEI 376 x TZEI 379	-55.13*	-56.79*	25.32	14.64	168.64*	133.84*
TZdEI 69 x TZEI 3A	-56.45*	-58.5*	-35.96	-36.00	79.55*	77.08*
TZEI 378 x TZdEI 272	-51.26*	-51.76*	178.06**	148.93*	122.4*	110.63*
TZdEI 69 x TZEI 298	-47.47*	-52.5*	113.13*	102.41*	291.1**	267.08**
TZEI 475 x TZdEI 40	-54.8*	-59.97*	89.64*	85.95*	202.32**	201.89**
TZdEI 272 x TZEI 376	-48.84*	-56.22*	6.28	-2.20	58.48	38.38
TZdEI 272 x TZdEI 192	-48.47*	-48.96*	-21.24	-26.28	42.64	34.22
TZdEI 272 x TZdEI 124	-65.83*	-68.03*	100.72*	66.89	476.52**	352.67**
TZEI 127 x TZEI 470	-62.54*	-63.27*	268.61*	233.49**	560.2**	472.61**
TZEI 472 x TZEI 449	-55.99*	-59.61*	96.85*	78.70*	296.25**	252.63**
TZEI 470 x TZEI 520	-56.55*	-58.71*	101.6*	82.72*	138.24*	120.34*
TZEI 3A x TZdEI 124	-56.32*	-58.71*	229.41*	213.51**	542**	491.45**
TZEI 402 x TZdEI 192	-59.48*	-65.73*	96.62*	77.81*	379.46**	301.23**
TZEI 475 x TZEI 468	-66.25*	-66.99*	161.24**	122.56**	255.05**	204.3**
TZdEI 192 x TZdEI 69	-64.17*	-65.28*	61.25	42.56	147.79*	115.74*
TZEI 3A x TZdEI 238	-53.37*	-54.16*	187.05**	186.77**	330.38**	323.29**

Appendix 12 Cont'd

TZEI 127 x TZEI 475	-54.64*	-57.8*	294.1**	246.00**	797.95**	681.65**
TZEI 485 x TZEI 456	-48.63*	-51.47*	113.34*	108.77*	306.31**	278.88**
TZdEI 124 x TZdEI 69	-45.47*	-52.1*	473.17**	444.40**	700.5**	689.84**
TZEI 497 x TZEI 520	-65.14*	-67.95*	173.03**	163.18**	654.47**	635.09**
TZEI 376 x TZdEI 216	-53.5*	-53.69*	478.45**	458.42**	738.22**	735.64**
TZEI 462 x TZEI 470	-57.37*	-57.73*	71.66	55.67	179.97**	165.23**
TZEI 378 x TZEI 298	-51.46*	-51.75*	-43.29	-46.69	100.73*	76.61*
TZEI 497 x TZdEI 40	-46.47*	-49.26*	163.29**	141.98*	403.58**	373.33**
TZEI 376 x TZdEI 283	-50.93*	-53.82*	39.30	33.71	254.63**	229.64**
TZEI 365 x TZdEI 216	-49.1*	-50.49*	140.2**	132.59*	580.9**	548.04**
TZdEI 215 x TZdEI 192	-53.05*	-57.65*	250.03**	210.15**	472.21**	385.89**

Appendix 13 Mean performance of the 156 hybrids evaluated across *Striga*-infested, low-N and optimal environments in 2016 and 2017

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment.	*Striga*infested	Low-N
TZdEI 216 x TZEI 3A	E1	6454.54	2987.88	2425.62	4262.10	53.71	62.42
TZdEI 124 x TZEI 379	E2	6896.42	3377.02	4975.68	5104.52	51.03	27.85
TZEI 470 x TZdEI 40	E3	5836.00	3124.04	2941.94	4172.40	46.47	49.59
TZEI 467 x TZEI 475	E4	4441.00	2538.32	4092.24	3610.18	42.84	7.85
TZEI 402 x TZEI 376	E5	3953.84	2521.30	1989.16	2987.88	36.23	49.69
TZEI 470 x TZEI 461	E6	5559.28	3212.74	3027.86	4114.38	42.21	45.54
TZEI 365 x TZdEI 69	E7	5095.36	2629.42	3389.62	3767.84	48.40	33.48
TZEI 378 x TZEI 402	E8	4734.44	2662.74	2948.16	3548.50	43.76	37.73
TZEI 467 x TZEI 497	E9	5362.74	2449.64	2304.80	3585.92	54.32	57.02
TZdEI 216 x TZEI 402	E10	5316.44	3896.08	3229.74	4330.96	26.72	39.25
TZdEI 69 x TZdEI 272	E11	5440.56	2841.90	2940.08	3901.00	47.76	45.96
TZdEI 215 x TZdEI 238	E12	3336.06	1981.80	2949.46	2717.04	40.59	11.59
TZdEI 216 x TZEI 298	E13	6182.70	2735.74	2581.56	4083.68	55.75	58.25
TZdEI 69 x TZEI 402	E14	5941.66	3032.74	2167.48	4023.26	48.96	63.52
TZEI 298 x TZdEI 124	E15	5881.98	2971.74	2849.62	4111.42	49.48	51.55
TZEI 8 x TZEI 468	E16	5840.34	2866.94	2171.24	3917.16	50.91	62.82
TZEI 379 x TZdEI 215	E17	6989.30	3425.88	3938.34	4953.74	50.98	43.65
TZdEI 216 x TZdEI 272	E18	6444.94	2497.12	4130.38	4402.90	61.25	35.91
TZdEI 216 x TZdEI 215	E19	4890.84	3783.86	3627.66	4195.42	22.63	25.83
TZdEI 272 x TZdEI 238	E20	5728.24	2827.64	2746.72	3971.70	50.64	52.05
Grand Mean		4992.70	2406.80	2652.64	3490.32	51.79	46.87
LSD		1939.98	1133.04	1676.36	957.56		
CV (%)		39.56	47.93	45.39	44.22		

Appendix 13 Cont'd

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*infested	Low-N
TZEI 520 x TZEI 127	E21	5101.52	2082.86	2207.92	3315.34	59.17	56.72
TZEI 378 x TZEI 3A	E22	5198.80	2828.84	1888.58	3588.78	45.59	63.67
TZEI 472 x TZEI 475	E23	4107.54	2059.88	1212.18	2709.40	49.85	70.49
TZdEI 40 x TZEI 467	E24	5452.82	2682.58	1699.40	3594.04	50.80	68.83
TZEI 462 x TZEI 449	E25	5593.16	1332.96	2689.20	3308.30	76.17	51.92
TZEI 468 x TZEI 462	E26	5465.60	2100.96	3479.56	3722.54	61.56	36.34
TZEI 485 x TZEI 467	E27	5474.42	1343.44	2523.30	3231.80	75.46	53.91
TZEI 3A x TZdEI 192	E28	6037.46	2848.28	4145.16	4383.32	52.82	31.34
TZdEI 192 x TZdEI 216	E29	6360.54	3026.82	4646.88	4684.32	52.41	26.94
TZEI 298 x TZdEI 192	E30	6079.46	2462.56	3092.04	4035.22	59.49	49.14
TZEI 127 x TZEI 449	E31	6783.26	4546.12	3979.04	5327.56	32.98	41.34
TZdEI 40 x TZEI 462	E32	6642.72	3483.68	1902.18	4431.00	47.56	71.36
TZdEI 40 x TZEI 127	E33	6331.68	2698.92	2214.74	4055.18	57.37	65.02
TZEI 365 x TZEI 379	E34	4287.52	2270.48	3275.04	3278.20	47.04	23.61
TZEI 402 x TZdEI 238	E35	4346.86	3106.92	2415.66	3464.64	28.52	44.43
TZdEI 215 x TZdEI 124	E36	7190.72	3000.34	3665.54	4809.52	58.27	49.02
TZEI 468 x TZEI 456	E37	4982.30	1866.36	1314.44	3002.36	62.54	73.62
TZdEI 40 x TZEI 472	E38	7859.72	2248.20	1406.42	4324.46	71.40	82.11
TZEI 497 x TZEI 461	E39	5298.28	2221.04	1722.64	3352.26	58.08	67.49
TZEI 456 x TZEI 8	E40	3570.74	2191.58	1283.58	2561.64	38.62	64.05
Grand Mean		4992.70	2406.80	2652.64	3490.32	51.79	46.87
LSD		1939.98	1133.04	1676.36	957.56		
CV (%)		39.56	47.93	45.39	44.22		

Appendix 1 Cont'd

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Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*infested	Low-N
TZEI 365 x TZEI 378	E41	4368.74	2184.32	2376.90	3096.60	50.00	45.59
TZEI 298 x TZdEI 238	E42	5035.84	2671.70	1537.28	3390.46	46.95	69.47
TZdEI 192 x TZdEI 283	E43	5501.84	3153.56	2145.90	3891.34	42.68	61.00
TZdEI 40 x TZEI 456	E44	5807.12	2823.38	2558.36	3963.86	51.38	55.94
TZdEI 238 x TZdEI 283	E45	5519.18	3117.30	4382.24	4331.04	43.52	20.60
TZEI 462 x TZEI 475	E46	4229.86	1603.76	1211.70	2575.78	62.08	71.35
TZEI 127 x TZEI 497	E47	6136.16	2442.68	4386.74	4308.88	60.19	28.51
TZEI 475 x TZEI 461	E48	2078.84	1832.96	90.38	1582.80	11.83	95.65
TZEI 449 x TZEI 468	E49	3967.72	2047.78	2952.16	2996.64	48.39	25.60
TZdEI 283 x TZEI 298	E50	5025.98	2732.70	451.74	3013.12	45.63	91.01
TZEI 467 x TZEI 449	E51	4972.64	2101.24	5313.22	3892.20	57.74	-6.85
TZEI 449 x TZEI 520	E52	2576.48	1187.34	1191.02	1743.74	53.92	53.77
TZdEI 238 x TZdEI 216	E53	4635.92	2971.24	2178.32	3478.54	35.91	53.01
TZdEI 69 x TZdEI 215	E54	6543.98	3364.80	4056.48	4774.80	48.58	38.01
TZEI 485 x TZEI 127	E55	4765.66	2338.76	2264.48	3294.66	50.92	52.48
TZEI 467 x TZEI 470	E56	2473.72	1408.24	596.20	1672.02	43.07	75.90
TZdEI 283 x TZEI 402	E57	3622.08	2514.26	2223.50	2899.24	30.59	38.61
TZEI 461 x TZEI 127	E58	5738.66	3810.98	1984.12	4216.68	33.59	65.43
TZEI 472 x TZEI 497	E59	4556.02	2467.12	1985.38	3206.34	45.85	56.42
TZEI 456 x TZEI 497	E60	3434.40	1861.68	2459.92	2610.42	45.79	28.37
TZEI 379 x TZEI 402	E61	4144.82	2469.84	2324.58	3110.78	40.41	43.92
Grand Mean		4992.70	2406.80	2652.64	3490.32	51.79	46.87

Appendix 13 Cont'd

LSD	1939.98	1133.04	1676.36	957.56
CV (%)	39.56	47.93	45.39	44.22

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*infested	Low-N
TZEI 8 x TZEI 485	E62	5527.70	2838.32	3140.06	3974.42	48.65	43.19
TZEI 462 x TZEI 8	E63	3873.74	2323.18	3180.84	3114.94	40.03	17.89
TZEI 461 x TZEI 462	E64	2068.08	1922.30	1240.36	1844.22	7.05	40.02
TZEI 449 x TZdEI 40	E65	5538.82	2628.26	3954.72	4057.78	52.55	28.60
TZdEI 283 x TZdEI 272	E66	5826.44	2253.14	3376.32	3907.10	61.33	42.05
TZEI 449 x TZEI 485	E67	3982.88	1728.80	1632.94	2611.26	56.59	59.00
TZdEI 124 x TZEI 378	E68	6084.26	3113.20	4159.70	4510.92	48.83	31.63
TZdEI 192 x TZEI 379	E69	6043.82	3385.62	3777.60	4527.30	43.98	37.50
TZdEI 272 x TZEI 365	E70	4111.24	2100.20	2224.20	2929.42	48.92	45.90
TZdEI 238 x TZEI 378	E71	6571.36	2097.50	2351.98	3937.94	68.08	64.21
TZdEI 124 x TZdEI 283	E72	7233.70	2496.10	4319.88	4755.90	65.49	40.28
TZEI 378 x TZdEI 215	E73	7797.52	3090.22	3895.62	5134.22	60.37	50.04
TZEI 298 x TZEI 365	E74	4344.26	1948.56	1417.34	2800.60	55.15	67.37
TZEI 379 x TZEI 298	E75	3468.58	2231.66	1791.36	2638.36	35.66	48.35
TZdEI 124 x TZdEI 216	E76	6105.04	2769.54	2362.18	4022.28	54.64	61.31
TZdEI 215 x TZEI 365	E77	5056.42	3255.54	4493.10	4223.40	35.62	11.14
TZEI 470 x TZEI 485	E78	3818.42	1946.68	2522.80	2810.60	49.02	33.93
TZEI 467 x TZEI 8	E79	4818.66	3096.28	2440.48	3654.08	35.74	49.35
TZEI 456 x TZEI 470	E80	5214.80	2113.24	1564.34	3244.08	59.48	70.00
TZdEI 192 x TZEI 378	E81	3199.04	2317.60	2802.82	2767.22	27.55	12.39
TZdEI 238 x TZEI 379	E82	5238.24	2069.34	3540.46	3631.12	60.50	32.41
Grand Mean		4992.70	2406.80	2652.64	3490.32	51.79	46.87
LSD		1939.98	1133.04	1676.36	957.56		

Appendix 1 Cont'd

CV (%)		39.56	47.93	45.39	44.22		

3

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*-	Lowinfested N
TZEI 485 x TZEI 462	E83	3548.10	2210.06	2198.40	2742.94	37.71	38.04
TZEI 470 x TZEI 468	E84	1142.18	3107.64	951.82	1733.88	-20.30	44.78
TZEI 461 x TZEI 456	E85	3200.46	1516.82	1959.76	2278.86	52.61	38.77
TZEI 462 x TZEI 497	E86	3119.50	1313.08	2130.42	2199.12	57.91	31.71
TZEI 127 x TZEI 8	E87	5349.08	1451.32	3112.94	3342.76	72.87	41.80
TZEI 3A x TZdEI 365	E88	4511.14	1437.28	2116.46	2802.66	68.14	53.08
TZEI 472 x TZEI 8	E89	5904.04	2347.70	3472.94	3995.28	60.24	41.18
TZdEI 283 x TZdEI 215	E90	7256.68	2530.86	2904.54	4495.92	65.12	59.97
TZEI 402 x TZEI 365	E91	4703.78	2398.30	1515.86	3144.00	49.01	67.77
TZEI 402 x TZdEI 124	E92	6322.00	3155.58	2683.84	4327.80	50.09	57.55
TZdEI 215 x TZEI 376	E93	5494.76	3314.20	3981.80	4319.94	39.68	27.53
TZdEI 238 x TZdEI 69	E94	5507.18	2341.60	2893.80	3718.28	57.48	47.45
TZEI 520 x TZEI 467	E95	2784.98	1269.44	2930.98	2207.96	54.42	-5.24
TZEI 376 x TZEI 378	E96	4639.26	1390.26	2087.80	2829.38	70.03	55.00
TZEI 365 x TZdEI 283	E97	4925.04	2518.86	3570.44	3691.64	48.86	27.50
TZEI 485 x TZEI 472	E98	3904.56	1804.64	3049.52	2893.58	53.78	21.90
TZdEI 283 x TZEI 3A	E99	3478.44	3100.94	2575.32	3146.82	10.85	25.96
TZEI 376 x TZEI 379	E100	3614.74	2953.64	2296.42	3086.64	18.29	36.47
TZdEI 69 x TZEI 3A	E101	5459.30	2539.92	3015.84	3802.86	53.48	44.76
TZEI 378 x TZdEI 272	E102	6926.08	3332.64	4262.12	4955.90	51.88	38.46
TZdEI 69 x TZEI 298	E103	4403.96	2048.80	2146.56	3010.42	53.48	
				2652.64			
Grand Mean		4992.70	2406.80		3490.32	51.79	
LSD		1939.98	1133.04	1676.36	957.56		
CV (%)		39.56	47.93	45.39	44.22		

5.26
46.87

Appendix 13 Cont'd

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*-Lowinfested N	
TZdEI 69 x TZEI 298	E103	4403.96	2048.80	2146.56	3010.42	53.48	51.26
TZEI 475 x TZdEI 40	E104	5600.56	2059.24	2194.98	3502.92	63.23	60.81
TZdEI 272 x TZEI 376	E105	6299.32	1827.80	4102.38	4071.32	70.98	34.88
TZdEI 272 x TZdEI 192	E106	5280.86	2179.16	4804.22	3944.84	58.73	9.03
TZdEI 272 x TZdEI 124	E107	5614.04	3828.54	3916.88	4560.40	31.80	30.23
TZEI 127 x TZEI 470	E108	5876.90	2057.96	2396.80	3653.30	64.98	59.22
TZEI 472 x TZEI 449	E109	5467.38	1925.44	2463.68	3449.86	64.78	54.94
TZEI 470 x TZEI 520	E110	2966.54	1898.52	771.94	2100.42	36.00	73.98
TZEI 3A x TZdEI 124	E111	5264.50	2513.28	2768.44	3664.80	52.26	47.41
TZEI 402 x TZdEI 192	E112	5479.10	2703.78	4240.38	4121.24	50.65	22.61
TZEI 475 x TZEI 468	E113	3216.98	2226.36	2077.28	2592.78	30.79	35.43
TZdEI 192 x TZdEI 69	E114	4178.16	1986.46	1934.02	2852.66	52.46	53.71
TZEI 3A x TZdEI 238	E115	5481.66	2727.92	1707.30	3625.30	50.24	68.85
TZEI 127 x TZEI 475	E116	5186.28	2636.68	2501.46	3629.48	49.16	51.77
TZEI 485 x TZEI 456	E117	5100.72	2472.80	2308.06	3491.02	51.52	54.75
TZdEI 124 x TZdEI 69	E118	4454.60	2469.82	4514.30	3672.62	44.56	-1.34
TZEI 497 x TZEI 520	E119	3874.60	1581.04	1979.20	2578.10	59.19	48.92
TZEI 376 x TZdEI 216	E120	4251.52	2793.46	3359.50	3489.90	34.30	20.98
TZEI 462 x TZEI 470	E121	4224.16	2260.94	1479.90	2890.02	46.48	64.97
TZEI 378 x TZEI 298	E122	4831.32	2248.70	1405.92	3113.18	53.46	70.90
TZEI 497 x TZdEI 40	E123	5775.28	2930.88	2278.02	3938.08	49.25	
				2652.64			
Grand Mean		4992.70	2406.80		3490.32	51.79	
LSD		1939.98	1133.04	1676.36	957.56		
CV (%)		39.56	47.93	45.39	44.22		

60.56
46.87

Appendix 1 Cont'd

Appendix 13 Cont'd

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*-Lowinfested N	
TZEI 376 x TZdEI 283	E124	5850.58	2118.78	2313.36	3650.42	63.79	60.46
TZEI 365 x TZdEI 216	E125	5803.28	2677.16	3757.74	4143.72	53.87	35.25
TZdEI 215 x TZdEI 192	E126	7543.50	2096.08	3896.04	4635.04	72.21	48.35
TZEI 298 x TZEI 376	E127	2630.36	1422.86	1923.28	2005.94	45.91	26.88
TZEI 3A x TZEI 376	E128	4833.04	1234.42	2467.96	2920.58	74.46	48.94
TZEI 376 x TZdEI 69	E129	11679.22	2474.68	4307.04	6522.96	78.81	63.12
TZEI 472 x TZEI 470	E130	2349.52	2663.12	221.22	1756.54	-13.35	90.58
TZEI 468 x TZEI 472	E131	3341.46	2157.32	688.70	2481.04	35.44	79.39
TZEI 475 x TZEI 485	E132	4367.46	1740.34	1514.38	2763.32	60.15	65.33
TZEI 8 x TZdEI 40	E133	6921.50	2265.94	2915.72	4396.20	67.26	57.87
TZEI 520 x TZEI 472	E134	4096.84	2201.76	2864.02	2881.44	46.26	30.09
TZEI 379 x TZdEI 272	E135	6599.20	1931.22	3510.42	4813.90	70.74	46.81
TZEI 475 x TZEI 520	E136	4373.42	2516.80	1718.30	2661.12	42.45	60.71
TZEI 497 x TZEI 485	E137	2674.36	1783.66	3885.68	2566.22	33.31	-45.29
TZEI 520 x TZEI 462	E138	4300.54	2611.16	2621.20	2932.14	39.28	39.05
TZEI 8 x TZEI 520	E139	4611.40	1674.74	4648.72	3776.80	63.68	-0.81
TZEI 468 x TZEI 127	E140	5427.98	3680.34	4034.32	4282.02	32.20	25.68
TZEI 497 x TZEI 468	E141	6294.30	1420.20	2641.20	4006.16	77.44	58.04
TZEI 456 x TZEI 449	E142	5247.94	1798.34	4280.50	3921.54	65.73	18.43
TZEI 456 x TZEI 475	E143	5190.20	1719.20	3173.78	3582.88	66.88	38.85
TZEI 461 x TZEI 467	E144	3519.04	2506.22	1887.78	2676.38	28.78	46.36
Grand Mean		4992.70	2406.80	2652.64	3490.32	51.79	46.87
LSD		1939.98	1133.04	1676.36	957.56		
CV (%)		39.56	47.93	45.39	44.22		
Check 6 - local check	E156	5991.68	1373.80	1445.46	3235.28	77.07	
				2652.64			

Appendix 13 Cont'd

Pedigree	Code	Grain yield (Kg ha^{-1})				Yield reduction due to stress (%)	
		Optimal	*Striga*	low-N	Across environment	*Striga*-Lowinfested N	
TZEI 461 x TZEI 467	E144	3519.04	2506.22	1887.78	2676.38	28.78	46.36
TZEI 8 x TZEI 461	E145	3327.78	3259.92	1164.18	2389.22	2.04	65.02
TZEI 468 x TZEI 467	E146	2330.10	2400.48	1430.40	1610.14	-3.02	38.61
TZEI 461 x TZEI 472	E147	3962.78	2415.68	1537.62	2587.44	39.04	61.20
TZEI 449 x TZEI 461	E148	3075.10	2180.12	2047.80	2260.66	29.10	33.41
TZEI 379 x TZEI 3A	E149	4598.66	2227.98	1751.86	2782.58	51.55	61.90
TZEI 520 x TZEI 456	E150	3782.98	2063.20	2249.98	2796.54	45.46	40.52
Check 1 - Kunjor-Wari	E151	4752.38	980.06	2882.74	3542.74	79.38	39.34
Check 2 - Suhudoo	E152	6544.06	1737.02	2995.68	4079.68	73.46	54.22
Check 3 - TZEI 124 x TZEI 25	E153	4532.96	1552.66	4231.76	3355.68	65.75	6.64
Check 4 - TZEI 60 x TZEI 86	E154	5773.50	1481.84	1637.30	3543.24	74.33	71.64
Check 5 - TZEI 129 x TZEI 16	E155	3782.44	2083.40	2039.72	2801.62	44.92	46.07
Grand Mean		4992.70	2406.80		3490.32	51.79	75.88
LSD		1939.98	1133.04	1676.36	957.56		46.87
CV (%)		39.56	47.93	45.39	44.22		