Genetic Analysis for Drought Tolerance and Yield Stability in Interspecific and *Oryza sativa* L. Rice Germplasm

by

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Thesis Abstract

Rice is currently an important staple food crop in Kenya. However, consumption continues to outstrip production. In spite of this, the country is endowed with untapped virgin land for rice production under rainfed upland and lowland ecologies. Nonetheless, drought, lack of modern improved farmer preferred cultivars, poor agronomic practices, and continued cultivation of low yielding late maturing landraces, are among the major challenges to rice production and expansion in the country. The objectives of this study were to: 1) document farmers' desired traits in rice cultivars and perceptions of rice production constraints in coastal region of Kenya, 2) identify drought tolerant rice genotypes at reproductive growth stage among the popular landraces, local cultivars, and exotic interspecific and *Oryza sativa* L. lines, 3) determine the inheritance of earliness and combining ability effects for phenological and morphological traits in rice under drought and no drought stress conditions, 4) determine the combining ability effects for grain yield and related traits in rice under drought and no drought stress conditions, 5) assess the heritability, correlation and the direct and indirect effect of phenological, morphological and yield component characters on grain yield and 6) estimate the magnitude of genotype x environment interaction (GEI) for grain yield in rice. The study period was between January 2013 and March 2015.

Farmers' desired traits in rice cultivars and perceptions of rice production constraints in coastal region of Kenya were assessed using formal household survey and participatory rural appraisal (PRA) methodology during 2013 and 2014. Data were collected from Msambweni Sub-county of Kwale County and Kaloleni sub-County of Kilifi County of coastal region of Kenya from a total of 326 respondents. The results established that farmers preferred high yielding, short duration and drought tolerant cultivars of medium height with white, long and bold grains. Preference for cultivars with good baking qualities was one of the unique traits that featured in this study. Important traits for a variety with good baking qualities were; white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin while baking. Drought was ranked as the most important constraint and drought stress occurring at reproductive and grain filling stage was the most prevalent. These findings reveal that an opportunity exists in the coastal region to breed for high yielding, early maturing drought tolerant cultivars with white, long, bold, tasty and aromatic grains, good for confectionery purposes.

Genetic variability for drought tolerance at reproductive stage was assessed among 21 rice genotypes comprising of 6 interspecific and 15 *Oryza sativa* genotypes. These were evaluated at KALRO-Mtwapa in pot experiments under two conditions of no drought and drought between April 2013 and March 2014. For each treatment, the experimental design was randomized complete block design with four replications and the plot size made up of 10 pots. Data collection included canopy temperature, relative leaf water content, leaf rolling and drying, days to 50% flowering, spikelet fertility and grain yield per plant. Considerable genetic variability for drought tolerance at reproductive stage existed among the interspecific and *Oryza sativa* L. rice lines. Two local *Oryza sativa* cultivars, Shingo la Mjakazi and Kitumbo were moderately drought tolerant. The interspecific genotype CT16323-CA-25-M was highly drought tolerant while NERICA 2 was moderately tolerant. These genotypes were identified as potential donors for drought tolerance at reproductive stage and may be used in breeding programmes aimed at developing drought tolerant cultivars for the rainfed lowland and upland ecologies in sub-Saharan Africa.

Inheritance and combining ability effects for earliness, grain yield and its contributing traits were studied using 10 x 10 half diallel mating design. The 10 parents included five interspecific and five *O. sativa* L. lines. The resulting F_1 progenies were advanced to F_3 generation. The 45 F_3 populations, 10 parents and one check were evaluated in 7 x 8 alpha lattice design with two replications under three no drought and one random managed drought stress conditions at three sites in coastal region of Kenya. Inheritance of earliness was found to be conditioned by non-additive gene action under random drought conditions and additive gene action under no drought conditions. One interspecific line CT16323-CA-25-M and one *O. sativa* line, Vandana, consistently exhibited desirable general combining ability for earliness under drought and no drought conditions. In addition, Vandana, was a good general combiner for grain yield and spikelet fertility under no drought conditions. Across environments, the line *Dourado precoce* had the best general combining ability effect for a thousand grain weight. The interspecific line, NERICA 2, was the best for number of grains per panicle while NERICA 1 had the best general combining ability effects for heavy panicle weight and weight of grains per panicle, and good grain phenotypic acceptability. Therefore these parents (CT16323-CA-25-M, Vandana, *Dourado precoce*, NERICA 2 and NERICA 1) may be hybridized with the intent of selecting promising genotypes within the segregating generations. The best F_3 populations with desirable specific combining ability effects were CT16323-CA-25-M x Vandana and Duorado x Vandana combining short duration with increased plant height and higher tiller number and NERICA 1 x NERICA 2 combining moderate drought tolerance index with desirable alleles for high yields, high thousand grain weight, heavy panicle weight, heavy grains per panicle and a good grain phenotypic acceptability. Early generation testing in these crosses was recommended to identify plants with desirable characters that may be advanced to homozygosity followed by selection of best pure lines for release in the region.

The narrow sense heritability estimates for earliness based on days to heading was high (67%), indicating predominance of additive gene action while that for grain yield was low (0.1%) implying predominance of non-additive gene action. Direct effects on grain yield were significant and positive for number of productive tillers per plant (P = 0.71), panicle weight (P = 0.66) and spikelet fertility (P = 0.49). However, the heritability estimates for number of productive tillers per plant (29%) were moderate, and low for panicle weight (0.7%) and spikelet fertility (4%) limiting their use in early generation selections. A thousand grain weight had a high narrow sense heritability (82%) and positive indirect effect (P =0.44) on grain yield via panicle weight indicating that improvement of grain yield may begin in early generations by indirectly selecting for high thousand grain weight via heavy panicle weight.

The stability analysis of the 45 F_3 populations and their parents over four environments using the AMMI and GGE biplot models showed that ranking of the genotypes changed across environments. This revealed a crossover type of genotype by environment interaction. Both AMMI and GGE biplot analyses showed that the four environments fell into three mega environments and identified G37 (Luyin 46 x IR55423-01) as the most high yielding genotype. However they differed on the most stable and high yielding genotype across the test environments. The AMMI analysis showed that G41 (NERICA-L-25 x Vandana) followed by G1 (NERICA 1 x NERICA 2) and G34 (CT16323-CA-25-M x Vandana) were the most stable and high yielding genotypes. In contrast, the GGE biplot showed that G39 (Luyin 46 x IR74371-54-1-1) followed by G40 (NERICA-L-25 x IR55423-01) were the most stable and high yielding genotypes.

Overall, this study provided valuable information that will help in setting and prioritization of breeding goals and objectives aimed at breeding for early maturing, farmer preferred cultivars, tolerant to drought stress at rice reproductive stage.

Declaration

I, **Ruth Nzisa Musila**, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other University.
3. This thesis does not contain other persons‘ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been re-written but the general information attributed to them has been referenced.
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5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the references sections.

Signed

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Ruth Nzisa Musila

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

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Dr. Julia Sibiya (Supervisor)

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Prof. John Derera (Co-Supervisor)

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Dr. John Kimani (Co-Supervisor)

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Dedication

This thesis is dedicated to my Heavenly Father with who there is no variation or shadow of turning; to my sons, Daniel and Joel, to my daughter Joy and my late father Mr. Joel Musila Kiilu

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Abbreviations

ACCI	African Centre for Crop Improvement
AEA	Average Environment Axis
AEC	Average Environment Coordinates
AGRA	Alliance for a Green Revolution for Africa
AMMI	Additive Main effects and Multiplicative Interactions
ANOVA	Analysis of Variance
AOE	Average Ordinate Environment
ARC	Africa Rice Centre (WARDA)
CEC	Cation Exchange Capacity
CIAT	International Center for Tropical Agriculture
CT	Canopy temperature
DA	Days to anthesis
DFL	Days to 50% flowering
DH	Days to heading
DM	Days to maturity
F_1	First filial generation
F_2	Second filial generation
F_3	Third filial generation
FAOSTAT	Food and Agriculture Organization of the United Nations – Statistics
GCA	General Combining Ability
GEI	Genotype by Environment Interaction
GGE	Genotype plus Genotype x Environment interaction
GPACP	Grain phenotypic acceptability
GPPN	Grains per panicle
GY	Grain yield
GYP^{-1}	Grain yield per plant
IRRI	International Rice Research Institute
KALRO	Kenya Agricultural and Livestock Research Organization
KARI	Kenya Agricultural Research Institute
LD	Leaf drying
LR	Leaf rolling
LSD	Least Significant Difference
MoA	Ministry of Agriculture

NERICA	New rice for Africa
NGPP	Number of grains per panicle
P	Phenotypic Path Coefficient
p	Probability level
PCA	Principal Component Analysis
PH	Plant height
PNL	Panicle length
PNWT	Panicle weight
PRA	Participatory Rural Appraisal
r	Pearson's correlation coefficient
R^2	Coefficient of determination
RCBD	Randomized Complete Block Design
RDI	Relative Drought Index
RLWC	Relative Leaf Water Content
SCA	Specific Combining Ability
SF	Spikelet fertility
SI	selection index
SPSS	Statistical Package for Social Sciences
SSA	Sub-Saharan Africa
TGWT	A thousand grain weight
TLA	Tiller number
TNO	Productive tiller per plant
USAID	United States Agency for International Development
WARDA	West African Rice Development Authority
WTGPPN	Weight of grains per panicle

Introduction to thesis

Background

Rice *(Oryza spp.),* is the staple food for more than half of the world's population, contributing over 20% of the total calorie intake of humans (Seck *et al.*, 2012). The leading producers of this cereal are China, India, and Indonesia which together account for over 50% of the world's total production (FAO, 2015). In sub-Saharan Africa (SSA), rice is currently one of the rapidly growing food crops in production and consumption. In a span of ten years the cultivated area has almost doubled reaching 10 million hectares with current annual production of approximately 23 million tonnes (FAO, 2015). Rice grain produced is directly used for human consumption with average per capita consumption of 24 kg per year in SSA. Although significant increases in production have been realised, still consumption outstrips production resulting in huge deficits that are met through importation. Among the net rice importers in the region, West Africa is the leading, accounting for 74% of the total volume imports in SSA while East Africa accounts for 15% (WARDA, 2005). In East Africa, Kenya ranks first in importation indicating that rice has become one of the most important food crops in the country (MoA, 2009).

In Kenya rice is currently an important staple food. There has been an increase in the annual per capita consumption from 12% in the last decade (MoA, 2009) to the current 15% (FAO, 2015) compared to 4% for wheat and 1% for maize (MoA, 2009). In the year 2011, annual rice production was estimated at approximately 110,000 tonnes while consumption was about 350,000 tonnes per year (FAO, 2015). Since 2009, the import bill has doubled to about US$ 190 million per annum (FAO, 2015). In spite of this, there exists a vast potential for production of rice in the country with about 0.5 million hectares of land that can support irrigated production and further 1.0 million hectares for rainfed production. The country has exploited about 1% of the existing potential land area. Of this area, 70% is under government managed irrigation schemes while the remaining 30% is under rainfed ecosystems (MoA, 2009). In Kenya, the main rainfed rice producing areas includes Kwale, Kilifi, and Tana River districts (Coast region), Bunyala and Teso districts (Western region), Migori and Kuria districts (Nyanza region). Of these regions, the coast region is viewed as a key potential area for rainfed upland and lowland rice production (MoA, 2009).

Kenya's coast is endowed with untapped suitable virgin land for rainfed upland and lowland rice production. Increased production in these ecosystems may turn the region into a new frontier in rice farming significantly reducing the costly rice imports experienced in the country. However, rice production in this region is still under subsistence farming system by smallholder farmers who grow the crop on farms ranging from 0.1 to 0.8 ha. The majority of the farmers continue to grow their low yielding and late maturing landraces, as well as old and out-dated improved varieties. Moreover, the crop is grown under stress-prone environments with limited resources. Consequently, rice yields in the region have remained very low ranging between 1.4 t ha^{-1} (Kega and Maingu, 2008) and 2.7 t ha^{-1} (USAID, 2010), far below the optimum of about 5 t ha^{-1} (MoA, 2009), and the worlds average of 4 t ha^{-1}. These low yields constitute one of the main challenges to rice production in the region.

Constraints to rice production and productivity in the coast region include socio-economic (cultivation of traditional late maturing and low yielding varieties, poor agronomic practices and lack of certified seeds), biotic stresses (diseases such as rice blast (*Magnaporthe oryzae)* and abiotic stresses (low soil fertility, saline soils, and erratic and unpredictable rainfall). However, among all these constraints, drought is a major constraint limiting production and yield stability in the coast region of Kenya (Kega and Maingu, 2008; Kimani *et al.*, 2011).

Separate reports from the coastal (Kega and Maingu, 2008) and the central parts (Kimani *et al.*, 2011) of Kenya unanimously agree that drought is increasingly becoming an important constraint to rainfed rice production in the country. A study involving the analysis of rainfall anomalies and means of 39 years meteorological data from the coastal region indicate that the region is characterised by drought years occurring in succession of 2 to 3 years (Muti and Kibe, 2009; Muti and Ng'etich, 2009). These results revealed that the drought years occur in tandem with a climatic phenomenon, unique for the region, locally termed "June winds" caused by the East African low level jet stream. These winds bring abrupt drought conditions in the middle of the long rainy season between May and June coinciding with the most critical growth stages of cereal crops and causing yield losses of over 95% (Muti and Kibe, 2009).

Besides, the coastal region experiences a bimodal type of rainfall and the short rainy season can be used to bridge the annual food deficit gap. Nonetheless, the season lasts only three months and cannot sustain the current local cultivars to maturity due to terminal drought that occurs late in the season. It is anticipated that the frequency of crop failures are likely to increase, threatening food security in the region. For this reason there is need to develop early maturing, drought tolerant rice cultivars to fit in the long rain season (April to July) and extra early maturing cultivars of less than 100 days duration to fit in the short rain season

(October to December) thus counteracting the unusual drought conditions in the coastal region.

Development of drought resistant rice cultivars involves intensive screening of rice genotypes under drought condition. The reproductive stage is the most sensitive to water stress and grain yield of rice is reduced most when drought stress occurs during this stage. Methods developed to screen rice genotypes for drought resistance at reproductive stage range from managed field stress environments (Garrity and O'Toole, 1994; Pantuwan *et al.*, 2002) to pot experiments (Lilley and Fukai, 1994; Wade *et al.*, 2000) under full to semi controlled conditions in greenhouses or in open fields. Pot experiments used in this study eliminate the confounding effects of heterogeneity for soil and moisture supply commonly associated with field screening. Several morphological, physiological and integrative traits have been identified as indicators of drought resistance at reproductive growth stage in drought screening trials (Garrity and O'Toole, 1994; Lilley and Fukai, 1994; Lafitte *et al.*, 2003). A few physiological traits used in this study have been recommended for application in drought breeding programmes (Lafitte *et al.*, 2003). Among them are relative water content, canopy temperature, leaf rolling and leaf drying scores. Among the integrative traits, spikelet fertility is the main yield component affected when stress occurs during the reproductive stage (Ekanayake *et al.*, 1989; Lafitte *et al.*, 2003).

In Africa, one of the most successful developments of early maturing cultivars has been the development of interspecific fixed lines developed between *Oryza glaberrima* and *Oryza sativa* L. These lines are a potential source of germplasm for improvement of adapted and introduced cultivars for drought escape and drought avoidance. However, no attempts have been made to incorporate the drought escape trait or earliness into the locally adapted germplasm in the coastal region of Kenya where terminal drought during the short rain season has forced farmers to cultivate only one rice crop during the long rain season. In contrast, the *O. sativa* lines are known for high yields. Development and evaluation of progenies from the interspecific and *O. sativa* lines for the appropriate phenology under drought and no drought conditions may yield early maturing, drought tolerant and high yielding genotypes for release in the coast region. There is also no information on the genetic basis of earliness in crosses between interspecific and *O. sativa* lines. Besides, combining ability and heritability studies for phenology, grain yield and other yield components will provide guidelines for setting a rice breeding programme. Further, information on contribution of the phenological, morphological and yield attributing traits on grain yield will aid in devising the best selection criteria for yield improvement in the region.

In sub-Saharan Africa, significant genotype x environment interaction (GEI) for grain yield and other agronomic traits has clearly been demonstrated in studies involving evaluation of major field crops of economic importance. Genotype x environment interaction is the differential genotypic response to environmental changes (Romagosa and Fox, 1993). With significant GEI, differences between genotypes vary widely among environments. The crossover type of GEI manifested as rank order changes of the genotypes between environments is the most important to plant breeders (Fox *et al.*, 1997). It reduces the association between phenotypic and genotypic values complicating selection of superior cultivars and best testing sites for identifying superior and stable genotypes (Flores *et al.*, 1998). Consequently, progress in providing farmers with high yielding cultivars is slowed down (Ceccarelli *et al.*, 2006).

In many breeding programmes, enormous research work invested in variety development is wasted because farmers never adopt the varieties developed. The reason is that farmers' preferences and perceptions are rarely taken into consideration during the development process. Through farmer – researcher collaboration, farmers and breeders interact to set breeding objectives and priorities (Sperling *et al.*, 2001). Farmers provide information on their preferred cultivar (Sperling *et al.*, 2001) and occurrence and relative importance of prevailing production constraints (Diagne *et al.*, 2013). With this information the breeder can then fit the farmer desired plant into the target environment in terms of climatic and soil related factors, diseases and pest resistance. Participatory rural appraisal (PRA) tools are usually applied to determine farmers' perceptions and preferences. In order to expand rice production and enhance the adoption of new rice cultivars in the coast region of Kenya, a PRA was conducted to better understand farmers perceived rice production constraints, and the traits they would desire in new cultivars.

Rationale for the research

Although the coastal region is viewed as a key potential area for rainfed upland and lowland rice production, rice yields in the region have remained very low ranging between 1.4 t ha^{-1} and 2.7 t ha^{-1}, far below the potential yields of about 5 t ha^{-1}. Drought is a major constraint limiting rice production and productivity in the region. The long rain season is characterised by drought stress that occurs at the middle of the season while terminal stress occurs during the short rain season. Lack of early maturing cultivars for the short rain season has forced farmers in the region to cultivate only one rice crop during the long rain season. Moreover, the current farmers' varieties are late maturing and have proven to be low yielding as mentioned by farmers during a survey conducted in the region in 2013 and 2014 (Musila, Unpublished). Although irrigation may be a more sustainable way for drought mitigation, this may not be effective because rice irrigation is dependent on rainfall and in years of low rainfall, water supply is limited. In addition, implementation of irrigation schemes is very expensive and in most cases, it is never the first option. Most small-scale farmers cannot afford the required irrigation facilities. Therefore, development of early maturing, drought tolerant rice cultivars to fit in the long rain season (April to July) and extra early maturing cultivars of less than 100 days duration to fit in the short rain season (October to December) may be the best option for drought management in the region. However, crucial information such as farmers' requirements, sources of drought resistance, inheritance of earliness, combining ability and stability studies for grain yield are required to devise an appropriate breeding strategy.

The national rice breeding programmes in various countries in sub-Saharan Africa are currently using the interspecific fixed lines developed between O. glaberrima and O. sativa for improvement of their local germplasm. In addition, although the traditional landraces are late maturing and low yielding they possess many of the desired farmer preferred traits. Therefore, given the importance of the interspecific lines and the traditional landraces, this study aimed at screening these species for drought stress tolerance and associated physiological and integrative traits at the reproductive stage of rice growth. From the drought screening evaluations, potential parents were selected to be used in interspecific breeding for high yielding drought escape and avoidance rice cultivars for the region. Thus, the interspecific fixed lines were used as potential sources for improvement of adapted and introduced cultivars for drought escape. In contrast, the *O. sativa* lines are known for high yields. In order to devise and set guidelines for appropriate breeding strategy, this study provided information on the genetic basis of earliness and combining ability studies for phenology, grain yield and other yield component in crosses between interspecific and *O. sativa* lines under drought and no drought conditions. Stability studies provided information on genotypes with wide and specific adaptation and the best testing sites for future use in multi-locational evaluations in the region. Furthermore, there has been resistance in adoption of new rice cultivars in the coastal region because most of these cultivars do not possess the desired traits found in traditional landraces. Therefore, to expand rice production and enhance the adoption of new rice cultivars in the region, through farmer – researcher collaboration, this study aimed at documenting farmers perceived rice production constraints, and the traits they would desire in new cultivars.

Research objectives

1) To document farmers' desired traits in rice cultivars and perceptions of production constraints to rice production in coastal region of Kenya
2) To determine genetic variability for drought tolerance at reproductive growth stage among the popular landraces, local cultivars, and exotic interspecific and *Oryza sativa* L. lines
3) To determine gene action and inheritance of earliness in interspecific and *Oryza sativa* L. pure lines under drought and no drought conditions
4) To estimate the general and specific combining ability effects for grain yield and yield related traits in interspecific and *Oryza sativa* L. pure lines under drought and no drought conditions
5) To assess the heritability, correlation and the direct and indirect effect of phenological, morphological and yield component characters on grain yield in rice
6) To estimate the magnitude of genotype x environment interaction (GEI) for grain yield in rice

Hypotheses:

1) Small-scale farmers in coastal region of Kenya have specific preferences for rice cultivars and face various production constraints with drought being a major production constraint
2) There is considerable genetic variability and high levels of reproductive stage drought tolerance in the popular landraces, local cultivars, and exotic interspecific and *Oryza sativa* L. lines
3) Inheritance of the drought escape trait or earliness in rice is controlled by additive gene action and that great improvement for this trait can be achieved through simple recurrent selection procedures
4) There is a high combining ability among interspecific and *Oryza sativa* L. lines for grain yield and yield contributing traits
5) There is high heritability for grain yield in interspecific and *Oryza sativa* L. varieties and positive correlation and direct effects of phenological, morphological and yield characters on yield

6) Grain yield of rice is affected by changes in environments; but high yielding and stable genotypes across environments do exist

Thesis outline

This thesis consists of seven distinct chapters (Table 0.1) reflecting the number of activities related to the above-mentioned objectives. The referencing system used in the chapters of this thesis is based on the Crop Science journal. This is one of the recommended thesis formats by the University of KwaZulu-Natal.

Table 0.1: Thesis structure

Chapter	Title
-	Thesis introduction
1	Literature Review
2	Farmers' desired traits in rice cultivars and perceptions of production constraints in coastal lowlands of Kenya and their implications for breeding
3	Variability of rice genotypes during reproductive stage under drought and no-drought conditions
4	Inheritance of earliness in interspecific and *Oryza sativa* L. rice lines under drought and no drought conditions
5	Combining ability for grain yield and yield components in interspecific and *Oryza sativa* L. rice lines under drought and no drought conditions
6	Heritability, correlation and path coefficient analysis for earliness and grain yield in interspecific and *Oryza sativa* L. lines
7	Genotype x environment interaction and stability of grain yield in rice under drought and no drought conditions
-	General overview and conclusions of the thesis

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Chapter One

Literature review

1.1 Introduction

This literature review covers topics relevant to the research focus and provides the theoretical basis for the research. It gives a summary of drought stress as a major production constraint. Areas discussed include economic importance, mitigation strategies and effects of drought to the rice plant. Mechanisms for drought resistance are discussed in depth with emphasis on drought escape and avoidance. Drought screening methodologies and sources for drought resistance are reviewed. In addition, the review gives an insight into rice genetics as well as gene action controlling earliness, grain yield and yield components. Heritability studies of various traits, path coefficient analysis as well as stability analysis methods are also reviewed.

1.2 Genetics, taxonomy and diversity of the genus *Oryza*

The genus *Oryza* (*O.*) contains 23 species with the basic chromosome number of 12. Of these species, 21 are wild whereas two are cultivated (Khush, 1997; 2000). Nine of the wild species are tetraploid while the remaining species are diploid. The two cultivated species, *O. glaberrima* and *O. sativa,* are diploid 2n (2x = 24). However, these two species do not interbreed easily (Jones *et al.*, 1997). The genome formula for *O. glaberrima is* A_gA_g while *O. sativa* bears the AA genome formula (Khush, 2000). Useful genetic diversity exists between and within these two species (Sleper and Poehlman, 2006). *O. glaberrima* has limited variation and has no known subspecies. It can be distinguished by two major ecotypes; a floating photosensitive type and an early erect type. The photosensitive ecotype is grown in deep water and coastal mangrove areas, whereas the erect early ecotype is grown in upland or moderately submerged lowlands (Ghesquière *et al.*, 1997). The erect early type is a good source of variation for important abiotic stresses. It grows in areas of drought with very little rainfall, thrives well under low input conditions, demonstrates high weed competitiveness and is resistant to pests and diseases (Jones *et al.*, 1997; Johnson *et al.*, 1998). However, it is low yielding, shatters easily, difficult to mill, and lodges frequently (Sarla and Swamy, 2005). Due to its ability to withstand harsh conditions, *O. glabberima* has become one of the most important sources of drought tolerant alleles in African rice breeding programmes (Jones *et al.*, 1997).

In contrast, *O. sativa* is cosmopolitan and has a wide diversity. While this variety cannot withstand harsh climatic conditions, it has unique traits such as high yields, easy to mill, and does not shatter easily (Sarla and Swamy, 2005). These good attributes mostly preferred by farmers could be the reason why it is multinational. In addition, it is highly variable and classified into three ecotypes namely *indica, japonica* and *javanica* (Chang, 1976). The *indica* ecotype is sensitive to low temperatures and remains dormant for a long periods of time. Temperate *japonica* is resistant to high temperatures and has moderate tillering whereas the tropical type is relatively insensitive to photoperiod. *Javanica* has low tillering ability and does not shatter easily (Acquaah, 2007). The wealth of genetic diversity between and within the Asian and African rice is the basis of the wide adaptation of the cultivated rice to diverse production systems. Moreover, interspecific hybridization of *O. sativa* and *O. glaberrima* species has resulted in further diversification of the cultivated rice producing the NERICA cultivars that survive well under adverse climatic conditions (Jones *et al*., 1997).

1.3 Rice production ecosystems

Rice production ecosystems are classified according to the source of water supply and include deep-water, mangrove swamp, irrigated, rainfed lowland and rainfed upland ecosystem (Olembo *et al*., 2010). Under mangrove swamp and deep-water systems, rice seedlings are transplanted in anaerobic soil and may be directly seeded on ploughed aerobic dry soil. The irrigated rice is cultivated in anaerobic soils and relies entirely on irrigation water throughout the cropping season. Rice production under the rainfed lowland systems is cultivated in aerobic to anaerobic soils flooded with rainwater for at least part of the season. Unlike these four ecosystems, the rainfed upland rice is directly seeded on entirely aerobic dry flooded soils (Wade *et al*., 1999; Bouman *et al*., 2007).

The major rice ecosystems found in Kenya are the irrigated, rainfed lowland, and rainfed upland ecosystem. Rice productivity in these ecosystems is faced by various constraints. The major yield reducing factors in the irrigated ecosystem include blast, rice yellow mottle virus (RYMV), low soil fertility (Kimani, 2010) and salinity (Wanjogu *et al*., 2001) while drought is the major yield reducing factor in the rainfed lowland and upland ecosystem. Rice yields in the paddy system average about 4.7 t ha^{-1} (MoA, 2009) against the potential of 9 t ha^{-1} achieved by the dominion farms in Yala Swamp (USAID, 2010). In the rainfed lowland and upland ecologies yields range between 1.4 t ha^{-1} in drought years (Kega and Maingu, 2008) and 2.7 t ha^{-1} in good years (USAID, 2010) far below the optimum of about 5 t ha^{-1} (MoA, 2009). Therefore, in order to intensify and expand rainfed rice cultivation in the country breeding high yielding drought tolerant rice cultivars remains a priority.

1.4 Drought stress

1.4.1 Definition

Drought is limited water availability to meet crop water requirements resulting in limited productivity (Pandey *et al.*, 2007; Blum, 2011). It is an environmental event during which water availability is below what is required for the full expression of yield potential (Ceccarelli *et al.*, 2007). Drought is one of the major factors limiting crop production worldwide. The major determinants of drought are rainfall and its distribution.

1.4.2 Economic importance of drought

Long drought spells occurring during the critical growth stages of the crop significantly reduce productivity (Serraj *et al.*, 2011). Surveys conducted in India, China and Thailand to quantify the impact of drought stress on rice production reported that drought greatly reduces rice production and productivity resulting in severe economic losses that directly affect the small-scale farmers (Jongdee *et al.*, 2006; Bhandari *et al.*, 2007; Ding *et al.*, 2007; Prapertchob *et al.*, 2007). These studies reported that in moderate drought years, rice yield losses ranged from 9 to 45% (Ding *et al.*, 2007) and 100% in severe stress (Bhandari *et al.*, 2007). Within sub-Saharan Africa yield losses due to drought of up to 46% have been observed in Gambia (Diagne *et al.*, 2013). Moreover, in drought years, there is a reduction in the cultivated area because part of the rice land is substituted to more drought tolerant crops (Jongdee *et al.*, 2006). In addition, due to the risks involved there is reduction in the use of agricultural inputs such as fertilizer as well as labour (Bhandari *et al.*, 2007; Ding *et al.*, 2007; Prapertchob *et al.*, 2007; Bernier *et al.*, 2008). Consequently, household incomes are adversely reduced in the range of 24 to 58%; a large number of farmers fall back to poverty translating to increased poverty at the national level (Pandey *et al.*, 2007). Therefore, implementation of short and long term mitigation measures cannot be overemphasised.

1.4.3 Strategies for mitigating drought

Farmers have developed various strategies to cope with drought. Strategies developed depend on whether drought occurs early or late in the season. In case of an early drought, farmers delay or postpone planting, replant, reduce fertilizer use and substitute part of the rice land for other crops. The cost in response to these strategies is a drop in the rice yields (Pandey *et al.*, 2007). On the other hand, when drought occurs late in the season, farmers do not seem to have much flexibility in making management adjustment and yields are drastically reduced and may even lead to total crop failures (Pandey *et al.*, 2007). Irrigation is an effective way of mitigating drought. However, in areas where rice irrigation is dependent on rainfall it may not be effective because in years of low rainfall, water supply is limited (Kimani, 2010). In addition, implementation of irrigation schemes is very expensive and in most cases, it is never the first option. Besides, most small-scale farmers cannot afford small and minor irrigation facilities. Therefore, host plant resistance has been suggested as the best option to help mitigate the effects of drought stress on the rice plant.

Development of drought tolerant cultivars can effectively address the problem of frequent droughts in rainfed lowland and upland rice ecosystems (Bernier *et al.*, 2008; Verulkar *et al.*, 2010). This technology is cheap; costs farmers nothing extra to grow tolerant cultivar than to grow a susceptible one. Significant yield performance under both stressed and non-stressed environments are realised and the drought tolerant cultivar can be cultivated in all seasons without any yield penalties in the good years (Atlin, 2003; Jongdee *et al.*, 2006).

1.4.4 Effects of drought stress on rice during the reproductive stage

Rice is sensitive to drought stress at reproductive stage and any drought stress occurring at this stage can cause significant yield losses. At booting stage water stress reduces peduncle length and rate of elongation. Reduced peduncle elongation primarily predisposes reduction in the rate of panicle exsertion (Rang *et al.*, 2011; He and Serraj, 2012) resulting in either incomplete or failure of the panicles to exsert from the boot (Ekanayake *et al.*, 1989; Pantuwan *et al.*, 2002). As mature spikelets are retained inside the flag leaf sheath, growth, maturation, opening of spikelets and pollination is prohibited, increasing the flowering period (O'Toole and Namuco 1983). As drought stress progresses, desiccation of exposed lemma, palea, and the anthers is observed. Desiccated anthers appear shrivelled and dry, whereas desiccated glumes turn white. Severe desiccation of glumes and anthers contribute to reduced flowering hence high spikelet sterility (Ekanayake *et al.*, 1989). In addition, high spikelet sterility results from damaged and abnormal development of the reproductive organs (He and Serraj, 2012). Under water stress conditions, the succession of events in pollen and ovule development that lead to fertilization and eventual formation of seed are irreversibly affected significantly reducing grain yield (Ekanayake *et al.*, 1989; Liu *et al.*, 2006). Water stress occurring before and during heading inhibits the processes of pollen development at meiosis stage and anther dehiscence. At meiosis stage, water stress interferes with development of the microspores into mature pollen grains. The number of pollen grains produced per stigma is reduced (Liu *et al.*, 2006; Rang *et al.*, 2011) into a ratio of 8:1 compared to 31:1 under optimal conditions (Liu *et al.*, 2006).

Anther dehiscence is related to a series of processes including floret opening, dehiscence, pollen shedding, germination, pollen tube growth and fertilization and drought influences each of these steps (He and Serraj, 2012). According to Liu *et al.* (2006), inhibition of anther dehiscence seems to be due to a combination of degeneration of the endothelial cells and failure of the pollen to reach the critical size. These two events preclude the opening of the apical and basal pores of the anther thus pollen grains are not released from the pollen sac. In addition, due to increased tissue water deficits, anther dehiscence is prohibited by low turgor condition of the floral parts: Lodicule, filaments, anthers and stigma (Ekanayake *et al.*, 1989)**.** For the few pollen grains that may be shed, these may fail to germinate on landing on desiccated stigmatic surface. If germination occurs, the pollen tube may never reach the micropyle (Liu *et al.*, 2006). Likewise, the dehydration of the stigma results in arrest of the events that lead to production of female gametes. Fertilization and eventual formation of seed is therefore inhibited resulting into spikelet sterility thereby decreasing the number of grains produced per panicle and reducing the sink size during grain filling (Lilley and Fukai, 1994a; Boonjung and Fukai, 1996).

1.4.5 Mechanism of drought resistance at the reproductive stage of rice

The four common components of drought resistance in rice and other crops in general are drought escape, dehydration avoidance, dehydration tolerance, and drought recovery (Levitt, 1980; Fukai and Cooper, 1995; Blum, 2011). This review focuses on drought escape and drought avoidance which were used in this study.

1.4.5.1 Drought escape

Drought escape is a mechanism in which plants complete their growth cycle before onset of drought later in the season. In this mechanism, the plant is not exposed to stress and therefore no subsequent development of strain. It is an important component of breeding solutions in rainfed environments where drought is severe, predictable, and terminal. It relates to early maturing genotypes that escape the effects of water stress through synchronisation between plant phenology and a given profile of drought (Blum, 1982). In rice drought escape as an adaptive mechanism has been extensively used as an important yield component in drought prone areas (Fukai and Cooper, 1995; Jongdee *et al.*, 2006). According to Jongdee *et al.* (2006) severe drought occurring late in the season can cause 45–50% yield loss. Under these conditions, selection for earlier maturing varieties greatly improves grain yield because cultivars that flower early tend to have greater numbers of fertile spikelet’s than those that flower late in the season (Mackill *et al.*, 1996).

1.4.5.1.1 Early maturity in rice

The growth duration of rice commonly known as phenology is composed of three successive phases: vegetative growth phase, the reproductive growth stage, and the ripening phase (Chen *et al.*, 2006). In the tropics the reproductive phase is about 35 days while the ripening phase ranges from 30 to 35 days and both phases are relatively constant (Vergara and Chang, 1985; Saito *et al.*, 2009). However, the duration of the vegetative growth phase varies greatly among rice cultivars and largely determines the growth duration of a cultivar, especially in the tropics. Thus although the comparative maturity of rice can be expressed as days to heading or days to ripening, heading date (HD) as characterised by the vegetative growth phase is a key determinant for physiological maturity of rice (Jiang *et al.*, 2007). Various genetic manipulations of this phase have resulted in development of early maturing rice cultivars. Early maturing varieties have a natural advantage of drought escape in the later part of the crop cycle and fit well into multiple cropping systems (Dwivedi *et al.*, 1980). However, in extremely early maturing cultivars plant size and yield may be reduced because the plant has a shorter growth period to develop, manufacture and store nutrient materials.

Breeding for earliness has been the cornerstone for improving rice production under drought prone environments where drought is severe predictable and terminal. In India, Cauvery delta zone, the late receipt of water in the canals forced farmers in this region to skip the short duration crop and raise only a single rice crop. However, using a line x tester design, an attempt was made to identify superior donors for earliness. In this study, AD 95157 was found to be a high yielding and early maturing variety (Sunil, 2006) and has since been incorporated in the hybrid breeding programmes aimed at developing early maturing cultivars in the region. In this programme, AD 95134 x TRY 2 was found suitable for simultaneous improvement of earliness and yield potential. In Africa, one of the most successful developments of early maturing cultivars has been the development of NERICA varieties. The early maturity of NERICAs was contributed by the genetic background of donor varieties of Asian cultivated rice (*O. sativa* L.) (Fukuta *et al.*, 2012). These varieties, therefore, act as donors for earliness in upland rice breeding. However, no attempts have been made to incorporate this earliness into the locally adapted germplasm in the coastal region of Kenya where insufficient amount of rainfall in the short rain season has forced farmers in the region to cultivate only one rice crop during the long rain season.

1.4.5.2 Dehydration avoidance

Dehydration avoidance is the ability of plants to maintain a relatively high level of tissue hydration, despite exposure to soil or atmospheric water stress (Blum, 2011). Many morphological and physiological traits conferring dehydration avoidance have been studied.

However, only a few have been reviewed for the purposes of this study. These traits include relative leaf water content, canopy temperature, leaf rolling, and leaf drying. They reflect the internal water status under water stress conditions and have been used in drought screening trials as indicators of dehydration avoidance and for identification of drought resistant genotypes (Ingram *et al.*, 1990; Garrity and O'Toole, 1994; Lilley and Fukai, 1994b; Garrity and O'Toole, 1995; Bimpong *et al.*, 2011).

Leaf rolling is the initial dehydration symptom observable when rice and other cereals are exposed to water stress. As plant water deficit progresses, leaf desiccation and death follow beginning with lower leaves and proceeds upwards. Several researchers have shown that genotypic variation exists in expression of leaf rolling and death. In a study to investigate the response of leaf rolling in rice to decreasing leaf water potential in two rice cultivars; Kinandang Patong and IR28, O'Toole and Cruz (1980) reported that Kinandang Patong, an upland adapted cultivar, maintained higher dawn and midday leaf water potential than IR28 and that the degree of leaf rolling were linearly related to leaf water potential. They concluded that because of the simplicity of scoring for leaf rolling, it could be used to estimate leaf water potential, a less obvious effect of water stress. In another study among four rice cultivars evaluated under water stress conditions during the reproductive stage, Lilley and Fukai (1994b) found that cultivars differed with the most drought sensitive genotype Rikuto-Norin 12 showing rapid leaf rolling and leaf death. In yet another study visual scoring of stressed plants was found to be the best method of screening for drought resistance, and was most strongly correlated with grain yield (Ingram *et al.*, 1990). These studies indicate that the expression of leaf rolling and death vary among genotypes. Therefore, the traits are good indicators for drought tolerance in drought screening trials.

Relative leaf water content directly measures the actual water content of a leaf relative to its water content at full turgor (Blum, 2011; Mullan and Pietragalla, 2012). While investigating the response of different accessions of *O.glaberrima* to water stress, Bimpong *et al.* (2011) reported marked differences among the cultivars in relative leaf water content. Canopy temperature is an indirect measure of plant water status. In rice, Infrared thermometry of leaf canopies has been found to be very effective for drought resistance phenotyping (Ingram *et al.*, 1990; Garrity and O'Toole, 1995). In a study aimed at assessing canopy temperature response of different rice genotypes under water stress conditions during the reproductive growth stage, Garrity and O'Toole (1995) concluded that canopy temperature was useful in classifying rice cultivars for relative dehydration avoidance. Canopy temperature was found to be correlated with visual drought scores (Ingram *et al.*, 1990; Garrity and O'Toole, 1995).

The extent of tissue dehydration exemplified by dehydration avoidance of physiological traits greatly determines plant reproduction under reproductive stage drought stress conditions. Effects of drought stress on physiological traits reduce spikelet fertility and yield components and ultimately grain yield (Garrity and O'Toole, 1995). Several studies have shown that these physiological traits are correlated with grain yield and its components under drought stress conditions (Ingram *et al.*, 1990; Garrity and O'Toole, 1995; Babu *et al.*, 2003). For example, canopy temperature was found to be highly and significantly correlated with grain yield and spikelet fertility (Garrity and O'Toole, 1995). Ingram *et al.* (1990) also reported that canopy temperature and leaf rolling were most strongly correlated with grain yield. Contrary to this, Pantuwan *et al.* (2002) showed that canopy temperature, leaf rolling and death were less correlated with grain yield under drought stress conditions. Lack of association was attributed to lack of genetic variation in physiological traits. In conclusion, drought resistance in drought tolerant cultivars is not conferred by one trait but rather by expression of different physiological and morphological traits that directly or indirectly affect grain yield. The reviewed traits were also used in this study for identification of drought tolerant cultivars.

1.4.6 Drought screening methodology adaptable at the reproductive stage of rice

Protocols developed to screen rice germplasm for drought tolerance at reproductive stage range from managed field stress environments to pot experiments in screen and greenhouses to rainout shelters. A mass screening method that involves generating a controlled off season drought stress event during the flowering stage was proposed by Garrity and O'Toole (1994). In this method irrigation water is withheld during the flowering period to simulate drought. Materials of the same maturity group are planted simultaneously. On the other hand, staggered planting is used to effectively synchronise flowering of different maturity groups during the treatment period. Synchronisation is done to avoid the early maturing genotypes escaping the severity of the drought stress as compared to late maturing ones (Garrity and O'Toole, 1994).

Field-based screens for genetic variation in reproductive-stage drought tolerance are often confounded by heterogeneity of soil and moisture supply, genetic variation in root depth, flowering date and biomass at flowering (Lilley and Fukai, 1994b; Liu *et al.*, 2006). Comparing deep-rooted with shallow-rooted genotypes usually gives the deep rooted genotypes an advantage and overlooks novel drought tolerance traits that might not be expressed in field screens. Pot experiments that were used in this study eliminate the confounding effects commonly associated with field screening. Genotypes are planted in shallow containers to specifically eliminate the dehydration avoidance conferred on deep rooted genotypes (Liu *et al.*, 2006). Two deep-rooted upland tropical japonicas (Azucena and Moroberekan) are known to confer dehydration avoidance at vegetative stage simply because of their deep roots (Liu *et al.*, 2006). Liu *et al.* (2006) evaluated these two genotypes in shallow containers to assess their genetic variation in reproductive stage drought tolerance. The study showed that by withholding water for 6 days spikelet fertility was reduced by 80% in Azucena but by 22% in Moroberekan, a difference attributable principally to high anther dehiscence after drought recovery. Therefore, experiments performed with pot-grown plants along with staggered planting may be used to identify novel drought tolerant genotypes among genotypes that differ in flowering date and root morphology.

1.4.7 Genetic resources for drought tolerance in rice

The choice of genetic resource to use as donors for resistance to drought depends on the probability of discovering the desired genes as well as the ease of introgressing these genes into the chosen recurrent cultivar. In rice, sources for drought resistance have been found among wild, cultivated rice and landraces (Liu *et al.*, 2004; Zhang *et al.*, 2006). Among the wild species, several accessions of *O. longistaminata* and *O. rufipogon* have been shown to possess useful drought adaptive traits. For instance, SL313-13 and Ulanpur 18 accessions of *O. longistaminata* and *O. rufipogon* respectively, displays a combination of high stomatal conductance, leaf elongation and high osmotic adjustment under stress conditions (Liu *et al.*, 2004).

According to Zeven (1998), landraces are highly diverse populations and mixtures of genotypes with a high capacity to tolerate biotic and abiotic stress resulting in a high yield stability and an intermediate yield level under a low input agricultural system. Landraces are adapted to specific ecosystems and farmers select which landraces to grow for socio-economic reasons (Bajracharya *et al.*, 2006). In a genome-wide association study of 517 rice landraces, Huang *et al.* (2010) reported alleles for drought tolerance in chromosomes 1, 5, 6 and 11. Agnihotri *et al.* (2009) observed that the rice landraces in Kumaun region of the Indian Central Himalaya had higher stomatal conductance, transpiration rate, water use efficiency and chlorophyll content in comparison to an introduced variety VL-206. Compared to the wild species, landraces have a high genetic compatibility with the improved cultivars and therefore an attractive genetic resource for drought tolerance (Blum, 2011).

Sources of drought resistance have also been identified within the cultivated Asian rice. Liu *et al.* (2004) reported that some cultivated rice that include Azucena and WAB 56-50 possess alleles for improved root growth and distribution under water deficit. In a study involving 325 BC_2F_2 bulk populations, developed by backcrossing drought tolerance donors to elite recurrent parents, Lafitte *et al.* (2006) reported presence of cryptic genetic variation for drought tolerance even in the drought-susceptible cultivars. Besides, the cultivated African rice has long been identified as a source of drought resistance among other traits (Zhang *et al.*, 2006; Olembo *et al.*, 2010). It has, therefore, been utilised in interspecific crossings with the Asian rice producing another source of drought resistance within the NERICA cultivars (Lamo, 2009; Olembo *et al.*, 2010). The early maturity of NERICAs was contributed by the genetic background of donor varieties of Asian cultivated rice (*O. sativa*) (Fukuta et al., 2012). These varieties, therefore, act as donors for drought escape in rainfed rice breeding.

1.5 Combining ability

According to Griffing (1956), the concepts of general combining ability (GCA) and specific combining ability (SCA) were introduced early in the 20th century by Sprague and Tatum (1942). General combining ability (GCA) is the average performance of a line in a hybrid combination and specific combining ability (SCA) is the deviation of a particular cross from the average performance of the lines involved. GCA is associated with additive gene effects whereas SCA is associated with non-additive gene effects (Sprague and Tatum, 1942; Falconer, 1989). If the variance due to GCA is greater than SCA, this indicates predominance of additive over non-additive gene effects. The additive genetic variance is the chief cause of resemblance between relatives and therefore determines the responsiveness of a population to selection (Sleper and Poehlman, 2006).

According to Christie and Shattuck (1992) combining ability reveals reliable information on the combining potential of parents. Once identified the best parental combiners can be hybridized with the intent of selecting promising genotypes within the generation. In their review they also indicated that although F_1 data are normally analysed, data from F_2 and generations thereafter can give better estimates of GCA than F_1. In support of these remarks in a study involving seven diverse cultivars of bread wheat, Bhullar *et al.* (1979) reported that the GCA estimates were repeatable over generations and that the estimates from the F_2/F_3 generations gave better predictions than those from the F_1. In another study using half diallel mating design of seven rice parents where the F_1 and F_2 generations where evaluated simultaneously, Verma *et al.* (2003) reported that estimates of GCA and SCA and the best general and specific combiners were consistent over generations. The few studies reviewed suggest that in self-fertilizing crops predictions of combining abilities are not likely to be jeopardized when estimated in F_2 and the later generation. For this reason in this study, combining ability estimates were evaluated in F_3 generation.

1.6 Gene action

Most traits of economic importance in plant breeding are quantitative rather than qualitative in nature. Quantitative traits are controlled by many genes each contributing a small effect to the overall phenotype expression of the trait (Kearsey and Pooni, 1996). The way in which these genes function individually and/or in association producing the final product is termed gene action and can be partitioned into additive, dominance and epistatic effects (Bernardo, 2002; Sleper and Poehlman, 2006; Acquaah, 2007). Of these, additive gene action is the only one which is heritable and the main cause of resemblance between relatives (Conner and Hartl, 2004). It is fixable and a great genetic improvement in the trait under consideration is easily achieved through selection (Acquaah, 2007). Contrary to this, the dominance and epistasis interactions either reduce or enhance selection limits, but in general they distort predictions of genetic improvements (Kearsey and Pooni, 1996). Thus, knowledge of the type of gene action prevalent in a population is of paramount importance to plant breeders in determining breeding methodology, cultivar type and in the interpretation of quantitative genetic experiments (Lamkey and Edwards, 1999).

1.6.1 Estimating gene action

The estimation of gene action has been approached in two ways; generation mean analysis (GMA) and variance component approach. The GMA involve measuring means of different generations derived from two homozygous lines and interpreting the means in terms of different genetic effects (Bernardo, 2002**.** It provides information on the relative importance of additive, dominance and epistatic gene effects. Basically for the estimation of additive and dominance gene effects, a minimum of three families namely parents and F_1 generation are required (Mather and Jinks, 1984). However, to estimate non-allelic interactions effects and their magnitude, a minimum of six family means provided by the parents, F_1, F_2 and first backcross generation of a cross between the two true breeding lines are required. Generation mean analysis is useful when the parents are divergent: when most, if not all, of the favourable alleles are in one parent and the unfavourable alleles are in the other parent (Hallauer *et al.*, 1988; Bernardo, 2002). The major advantage with GMA is that errors are inherently smaller because means are estimated with greater precision than variances. However, an estimate of heritability cannot be obtained and one cannot predict genetic advance because estimates of genetic variances are not available (Hallauer *et al.*, 1988).

Estimation of gene action through the variance component approach involves estimating genetic components of variances and defining them in terms of gene action (Hallauer *et al*., 1988). Progenies for estimating these variances are usually generated from either the six basic generations or mating designs. Although the basic generations provide estimates of all genetic and environmental components of variances they are an inefficient design in obtaining reliable estimates of the components and variances particularly the dominance genetic variance (Kearsey and Pooni, 1996). Mating designs which are more efficient in estimating these components have therefore been developed to generate progenies that involve relationships among relatives having known genetic components of variance (Hallauer *et al.*, 1988). Of these designs, the two factor design such as diallel design, nested design, and factorial (NCII) design can adequately estimate the additive and dominance genetic variances which are used to interpret the relative importance of additive versus non-additive gene action (Bernardo, 2002). Compared to generation mean analysis, estimation of genetic variances allows further estimates of heritability and response to selection of the population. Thus in this study the variance component approach was used to estimate gene action for earliness, grain yield and other yield components in interspecific and *Oryza sativa* L. lines.

1.6.2 Gene action studies for earliness in rice

Studies on the inheritance of earliness in rice have mostly been based on direct analysis of genetic parameters (Dwivedi *et al.*, 1980; Chen *et al.*, 2006) and on GCA and SCA variances in diallel tables (Dwivedi and Pandey, 2012). In a study conducted at IRRI (Los Baños) involving early maturing cultivars, Li and Chang (1970) reported predominance of additive gene action in inheritance of earliness. Among diallel elite parents having a wide range of heading dates, Dwivedi *et al.* (1980) reported that non-additive gene action was more important than additive gene action in the inheritance of earliness. In crosses involving interspecific *indica-japonica* breeding lines, Chen *et al.* (2006) found that non-additive gene action was more important than additive gene action contributing 68% of the total genetic variation of heading date. Contrary to these studies, based on GCA and SCA variances estimated from diallel mating design involving *japonica* and *indica* elite lines of diverse maturity, Dwivedi and Pandey (2012) reported that both additive and non-additive gene action were important. However, estimation of the relative importance of GCA and SCA variances revealed that additive gene action played a major role in the inheritance of days to flowering in these lines. From these studies there seem to be no consensus on the type of gene action controlling earliness in rice. This implies that estimation of gene action for earliness from one population cannot be extrapolated to another population. Therefore, if a sound breeding methodology for earliness is to be determined, gene action and inheritance of this trait should be estimated for each individual population under the target population of environments. In addition, the literature reviewed did not find any studies on gene action conditioning earliness in the interspecific fixed lines developed between *Oryza glaberrima* and *Oyza sativa L*. this information is essential for improvement of adapted and introduced cultivars in the coastal lowland of Kenya for drought escape.

1.6.3 Gene action studies for grain yield and yield components in rice

Studies on gene action for grain yield and its associated characters have mostly been based on estimating components of variance due to general combining ability and specific combining ability (Jayasudha and Sharma, 2009; Lamo, 2009; Malarvizhi *et al.*, 2010). Some studies have concluded both additive and non-additive gene action were important (Kumar *et al.*, 2007b; Kumar *et al.*, 2007c). Others have revealed predominance of additive gene action over non-additive gene action (Lamo, 2009). Yet others have reported non-additive gene action was more important (Verma *et al.*, 2003; Verma and Srivastava, 2004; Kumar *et al.*, 2008; Jayasudha and Sharma; 2009, Malarvizhi *et al.*, 2010). In a line x tester study of four cytoplasmic male sterile lines and 22 male parents evaluated under aerobic conditions, Malarvizhi *et al.* (2010) reported inheritance of grain yield per plant, spikelet fertility, 100-grain weight and number of grain per panicle was largely controlled by non-additive gene action. Under anaerobic conditions, predominance of non-additive gene action for grain yield and spikelet fertility was also revealed (Jayasudha and Sharma, 2009). Furthermore, among interspecific progenies, Lamo (2009) reported that additive effects were more important than non-additive effects for spikelet fertility and grains per panicle under water stress and non-stress environments. These studies suggest no consensus amongst different studies on the type of gene action controlling inheritance of grain yield and yield components under water stress and no stress conditions. Therefore, it is imperative to assess the type of gene action controlling grain yield and its contributing traits in interspecific and O*ryza sativa* rice lines evaluated under drought and no drought conditions in the rainfed lowland and upland ecologies of coastal lowlands of Kenya.

1.7 Heritability for grain yield and yield components

Heritability is the proportion of observed phenotypic variation in a progeny that is attributable to the effects of genes (i.e. heritable) (Kearsey and Pooni, 1996; Sleper and Poehlman, 2006). It is a property of the trait, the population and the environment. Altering one of these factors results in different estimates of heritability (Acquaah, 2007). There are two different estimates of heritability; broad and narrow sense heritability, the latter which is the degree of resemblance between relatives is more useful to plant breeders as it determines response to selection. High heritability estimates correspond to additive gene action while low heritability estimates are indicative of non-additive gene action. Moreover, a trait with high heritability estimates indicates that the transmissibility of that trait from the parents to the progeny is high and that simple selection procedures may be employed to select for superior genotypes and *vice versa*.

In rice, estimates of heritability for grain yield and other yield components have mostly been based on broad sense heritability. Several studies in India (Babu *et al.*, 2003; Kumar *et al.*, 2007a; Verulkar *et al.*, 2010), Philippines (Venuprasad *et al.*, 2007; Bernier *et al.*, 2009) and China (Yue *et al.*, 2005) have reported moderate to high broad sense heritability estimates for grain yield under severe to very severe drought conditions. Babu *et al.* (2003) evaluated a doubled haploid population derived from a cross between CT9993 and IR62266 during the reproductive stage under severe drought and irrigated conditions and reported broad sense heritability estimates of 59% and 61% respectively. Using the same doubled haploid populations evaluated under similar conditions for three years, Kumar *et al.* 2007a reported estimates of 37% and 45% under severe drought and controlled conditions. Studies by Venuprasad *et al.* (2007) using random segregating $F_{2:3}$ populations derived from high yielding and drought tolerant parents showed that broad sense heritability estimates for yield at reproductive stage under non-stress and stress conditions were 43% and 67%, respectively. In yet another study involving random F_3 population's derived lines from a cross between upland rice (*Oryza sativa* L.) cultivars Vandana and Way Rarem, broad sense heritability estimates for grain yield under very severe and non-stress conditions of 70% and 23% respectively were reported by Bernier *et al.* (2009). Furthermore, under drought stress at reproductive stage, Verulkar *et al.* (2010) reported moderate to high heritability estimates for grain yield in early (53%), intermediate (73%) and late (74%) maturing rice genotypes. These studies suggest that the heritability estimates for grain yield differ from one population to another even within the same population evaluated under different environments.

On yield components, under upland rice ecology in south east Ethiopia, Akinwale *et al.* (2011) reported high to medium broad sense heritability estimates on days to heading, days to maturity, plant height, number of grains per panicle, panicle weight, number of panicles per m^2 and panicle length. Low broad sense heritability estimates were observed for the number of tillers per plant and 1000 grain weight. Babu *et al.* (2003) reported moderate to high estimates for days to heading, spikelet fertility, and grains per panicle (50%). Among these traits spikelet fertility was correlated with yield. Bernier *et al.* (2009) reported high broad sense heritability estimate and high negative correlation for days to flowering with grain yield. In another study, Efisue *et al.* (2009) reported moderate heritability estimates for plant height. Furthermore, high broad sense heritability estimates were reported for days to flowering in early (86%), intermediate (83%) and late (91%) maturing rice genotypes by Verulkar *et al*. (2010). These studies indicate lack of consistency in heritability estimates for yield and yield components in rice. Therefore, this current study aimed at determining broad and narrow sense heritability estimates for grain yield and yield components in interspecific and O*ryza sativa* L. rice lines. With this information appropriate breeding strategy will be devised for development of high yielding, early maturing cultivars for the coastal region of Kenya.

1.8 Correlation and path coefficient analysis

Grain yield is regarded as the primary character with the main breeding objective in all crops being high yield. However, direct selection for yield is not sufficiently effective due to its low heritability. The use of phenological, morphological and physiological traits commonly known as secondary traits, as indirect selection criteria for higher yields has often been suggested. Although correlation coefficients are very important in determining the relative contribution of each secondary trait to grain yield, they are insufficient in determining whether the traits affect grain yield directly or indirectly (Nandan *et al.*, 2010). Through path analysis, the correlation coefficient may be partitioned into components due to direct effect of a predictor variable upon its response variable and due to indirect effect(s) of a predictor variable on the response variable through another predictor variable (Dewey and Lu, 1959). Plant breeders use path analysis to identify traits that are useful as selection criteria to improve crop yield (Surek and Beser, 2003). Zou *et al.* (2005) using correlation and path analysis indicated that spikelet fertility was particularly important for grain yield with direct effect of P=0.60 under drought stress, while spikelet number per panicle contributed the most to grain yield (P=0.41) under well-watered condition. In another study Babu *et al.* (2012) using path coefficient analysis showed that panicle length and number of productive tillers per plant had the highest positive direct effect on yield. Most of the literature reviewed showed that positive and direct effects on grain yield were mostly of number of productive tillers (Ibrahim *et al.*; 1990; Babu *et al.*, 2012; Seyoum *et al.*, 2012); panicle weight (Samonte *et al.*, 1998), and spikelet fertility (Zou *et al.*, 2005; Seyoum *et al.*, 2012; Hasan *et al.*, 2014). In this study, correlation and path analysis were used to identify traits that had direct effects on grain yield in order to devise a multiple trait selection criteria for improvement of yield in rice.

1.9 Forward selection multiple regression analysis

Forward selection multiple regression analysis has been used to analyse yield on other traits (Augustina *et al.*, 2013). This model identifies which trait came into the model and left the model significant ($P<0.05$) after regression with the dependent trait (yield), starting from the most important trait, and followed by progressive addition of new traits in an interactive manner as an important yield component. The process "stops" whenever the sample partial correlation is non-significant as shown by the standard *F* test (Bendel and Afifi, 1977). Augustina *et al.* (2013) also used forward selection multiple regression analysis to identify traits that would most contribute to grain yield improvement in a rice breeding programme. Number of grains per plant, weight of roots and days to 50% heading were identified as the most important yield components that could improve rice yield. This method has also been used in this study to identify traits that contributed the most to grain yield.

1.10 Genotype x environment interaction

Genotype x environment interaction (GEI) is the response of genotypes to environmental changes. It is expressed when the genotypic and environmental effects differ in accordance with the genotype and specific environment. Differential performance of genotypes is caused either by differential responses of the same set of genes to changes in the environment or by expression of different sets of genes in different environments. The norm of reaction is that genotypes are manifested either as rank order changes of the genotypes between environments (crossover GEI), or as alterations in the absolute differences between the genotypes without affecting the rank order (Crossa *et al.*, 1995; Bernardo, 2002). The crossover interaction results in serious consequences on breeding progress (Cooper and Delacy, 1994; Crossa *et al.*, 1995). For example the same set of genes responsible for high yield under stress environment may be responsible for low yield potential. In this case breeding progress is delayed due to changes in the composition of the selected and the rejected genotypes in each environment. In such cases, genotypes must be bred for specific adaptation to certain environments.

Large G X E interactions commonly occur under drought stress conditions as a result of variation in timing of water deficit, variation due to severity of water deficit and their interaction with nutrient deficiencies, and variations within the season and within the same field. This reduces heritability hence the breeding progress. Under such circumstances, plant breeders desire to find stable genotypes that show little interaction with environments (Yan *et al.*, 2007). An appropriate stable cultivar is capable of using resources that are available in high yielding environments, while maintaining above average performance in all other environments (Finlay and Wilkinson, 1963).

Methods for analyses and interpretation of G x E interactions patterns include regression (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966), Principal Component Analysis (PCA) (Hill and Goodchild, 1981), Additive Main Effects and Multiplicative Interaction (AMMI) (Gauch and Zobel, 1988) and Genotype plus Genotype by Environment (GGE) analysis (Yan, 2001). Of these, AMMI and GGE bi-plot are widely used. The AMMI model integrates analysis of variance (ANOVA) and principal component analysis (PCA) into a unified approach that can be used to analyse multi-location trials (Crossa *et al*., 1995; Gauch and Zobel 1988; Zobel *et al*., 1988). In AMMI1 a biplot of main effects with interaction PCA1 (IPCA1) facilitates visualisation of correlation among environments and the response patterns of the genotypes and their interactions with the environments by using sign and magnitude of IPCA1 values (Yan and Hunt, 2001). In AMMI2 a biplot of IPCA1 and IPCA2 is constructed which visualises magnitude of interaction for each genotype and environment

The GGE biplot analysis on the other hand puts together genotypic main effects (G) and G x E interaction to facilitate graphical visualisation of cultivar evaluation and mega environment identification (Yan *et al.*, 2000, Yan, 2002). The GGE biplot is constructed by the first two symmetrically scaled principal components (PC1 and PC2) derived from singular value decomposition (SVD) of environment centred data (Yan *et al.*, 2000, Yan, 2002). This biplot is useful in visualisation and identification of the mega environments, specific and wide cultivar adaptations, high yielding and stable cultivars and interrelationship among environments (Yan, 2001).

In rice the AMMI and GGE biplot analyses have been used to reveal presence of significant GEI in multi - locational trials. For example, in a study involving 16 upland rice genotypes evaluated in six environments in north-west Ethiopia, significant GEI was revealed by both AMMI and GGE analyses and stable and high yielding genotypes were identified (Lakew *et al*., 2014). Also, Sanni *et al*. (2009), while evaluating 22 NERICA cultivars in three environments in two years in West Africa, using the AMMI analysis, found the existence of a significant GEI with the first four IPCA's contributing 98.5% of the total interaction sum of squares. In yet another study involving rice germplasm evaluated in five environments in South-West Africa, the AMMI analysis revealed significant GEI for grain yield and panicle attributes. On grain yield, the first PCA axis of the interaction captured 52% of the interaction sum of squares while the GGE biplot captured 64% of the interaction component (Nassir, 2013). These studies show that environments in sub-Saharan Africa fluctuate considerably across sites and seasons. Therefore, assessment of genotype x environment interaction (GEI) in cultivar development in this region cannot be ignored.

1.11 Participation breeding

In many breeding programmes, enormous research work invested in variety development is wasted because farmers never adopt the varieties developed. The reason for the poor adoption of new varieties is that farmers' preferences and perceptions are often not taken into consideration during the development process (Efisue *et al.*, 2008). Farmer participation allows interactive breeding between the farmers and the scientists (Sperling *et al.*, 2001; Morris and Bellon, 2004). Farmers provide information on their environment and preferred varieties (Sperling *et al.*, 2001). The breeder then utilises this information to produce relevant varieties thus increasing their adoption (Joshi *et al.*, 2007). Although there are various approaches, participatory plant breeding and participatory varietal selection, are the mostly commonly used in rice breeding (Sié *et al.*, 2010). In the former, farmers are involved in implementation and designing of the breeding programmes (Ceccarelli *et al.*, 2007; Sié *et al.*, 2010) whereas in the later they are involved in the varietal evaluation and selection of the finished product (Sié *et al.*, 2010). Both of these approaches are highly client oriented and adequately meet farmers' requirements. However, they can be preceded by participatory rural appraisals (PRA) (Virk *et al.*, 2002).

Numerous PRA studies especially in sub-Saharan Africa have revealed that rarely do the local farmers' well defined plant ideotype which they seem to prefer correlate with that of scientists (Efisue *et al.*, 2008). Cultivar traits commonly targeted in conventional breeding system include high yielding, early maturing, fertilizer responsiveness and dwarfness (Morris and Bellon, 2004). However, a PRA study in Sikasso Region of Mali revealed that farmers in the upland and lowland rice ecologies preferred tall varieties and were willing to trade-off yield for grain quality and plant height (Efisue *et al.*, 2008). In contrast farmers in the irrigated ecology preferred high-yielding, long duration rice varieties (Efisue *et al.*, 2008). In the Ashanti region of Ghana, farmers preferred not only high yielding varieties but varieties that had specific grain quality attributes such as white coloured, long, slender and translucent grains (low chalkiness), fragrance and preferred cooking quality (Asante *et al.*, 2013). From these studies, it can be concluded that farmers' are well aware of their cultivar needs and prioritize traits depending on their preferences and prevailing environmental conditions. To increase the chances of adoption of modern rice varieties especially in the marginal areas, it is imperative that farmers' priorities and needs are treasured and incorporated in the breeding process.

1.12 Summary

From the literature review it is apparent that drought is a major constraint to rice production under rainfed upland and lowland ecologies in sub-Saharan Africa. Yield losses of up to 50% in moderate drought years and 100% during periods of severe drought have been reported in many parts of the world including Africa. Breeding for drought tolerance has been suggested as the most practical option to effectively address the problem of frequent droughts in rainfed lowland and upland rice ecosystems. Breeding for drought tolerance is approached in terms of its components. In rice, breeding for dehydration avoidance and drought escape are the common breeding strategies used in development of drought tolerant cultivars. Although there are many morphological and physiological traits conferring dehydration avoidance, only a few traits such as relative leaf water content, canopy temperature, leaf rolling, and leaf drying have been recommended as indicators of dehydration avoidance in drought screening trials. These traits may be used by plant breeders in identification of drought tolerant genotypes among the popular landraces, local cultivars, and exotic materials.

Inheritance of the drought escape trait or earliness as characterised by heading date was shown to be controlled quantitatively or polygenically. Gene action studies on earliness have suggested that both additive and non-additive gene action were important. Others have revealed predominance of additive gene action over non-additive gene action. Yet others have reported non-additive gene action was more important. The literature reviewed did not find any studies on gene action conditioning earliness in the interspecific fixed lines developed between *Oryza glaberrima* and *Oyza sativa L*. Yet these lines are a potential source of germplasm for improvement of adapted and introduced cultivars for drought escape. In addition, there is limited information on the type of gene action controlling grain yield and other yield components in crosses between interspecific and *Oryza sativa* L. lines. Therefore genetic studies on earliness, grain yield and yield components in interspecific and *Oryza sativa* L. lines under drought and no drought conditions are important in order to devise an appropriate breeding strategy aimed at developing high yielding drought escape and drought avoidance rice cultivars for the rainfed lowland and upland ecology in coast region of Kenya.

In this review it was noted that under drought stress conditions, large genotype x environment interactions (GEI) are common. A significant GEI especially the crossover type may delay progress in providing farmers with new cultivars. Multi-locational trials are, therefore, needed to determine the magnitude of GEI and to assist in identification and recommendation of high yielding and stable genotypes that show little interaction with the environment or genotypes specifically adapted to certain environments. Farmer – researcher collaboration was found to be the best strategy for enhancing adoption of new cultivars.

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Chapter Two

Farmers’ desired traits in rice cultivars and perceptions of production constraints in coast region of Kenya and their implications for breeding

Abstract

Production of rice in coastal lowlands of Kenya is still under subsistence farming system by smallholder farmers. The majority of the farmers’ continue to grow low yielding and late maturing landraces, old and out-dated unimproved varieties. As a result, rice yields in the region have remained extremely low ranging between 1.4 t ha^{-1} and 2.7 t ha^{-1} far below the worlds average of 4.0 t ha^{-1}. The objective of this study was to identify the smallholder farmers’ preferred rice characteristics and analyze and prioritize perceived rice production constraints in the selected rainfed lowland ecology. Data were collected from Msambweni Sub-county of Kwale County and Kaloleni Sub-County of Kilifi County of coastal region of Kenya from a total of 326 households using structured survey and participatory rural appraisal (PRA) methodology during 2013 and 2014. Results indicated high grain yield as the most preferred trait followed by short duration and drought tolerant cultivars. On plant height, the majority of the farmers (59%) preferred medium height varieties. However, farmers were willing to trade off medium plant height for grain quality traits. Although farmers prioritized the grain quality traits with aroma and taste being the most preferred, overall, the grain had to be white, long and bold. One of the unique preferences that featured in this study was that of cultivars with good baking qualities. Farmers highlighted the important traits for a variety with good baking qualities as: white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin while baking. On constraints, drought was ranked as the most important constraint and drought stress occurring at reproductive and grain filling stage was the most prevalent. These findings reveal that a need exist in the coastal region to breed for high yielding, early maturing drought tolerant cultivars with white, long, bold grains which incorporate the quality traits preferred by farmers.

Key words: Farmer preferred traits, participatory plant breeding, production constraints, rice landraces

2.1 Introduction

The Kenya's Coast is endowed with untapped suitable virgin land for rice production and irrigation water from the rivers Tana and Umba. Coupled with the available traditional knowledge of the local communities, proper utilization of these resources may turn the region into a new frontier in rice farming, significantly reducing the costly rice imports. However, rice production in this region is still under subsistence farming system by smallholder farmers who grow the crop on farms ranging from 0.1 to 0.8 ha. Majority of the farmers continue to grow their low yielding and late maturing landraces, as well as old and out-dated unimproved varieties. Moreover, the crop is grown under stress-prone environments with limited resources. Consequently, rice yields in the region have remained very low ranging between 1.4 t ha^{-1} (Kega and Maingu, 2008) and 2.7 t ha^{-1} (USAID, 2010), far below the optimum of about 5 t ha^{-1} (MoA, 2009). These yields are similar to those reported in the rest of sub-Saharan Africa (SSA), which averages 1.5 t ha^{-1} far below the worlds' average of 4 t ha^{-1} and constitute one of the main challenges to rice production in SSA.

Rice productivity in SSA is limited partly by abiotic and biotic factors which vary significantly across growing environments and countries. Among the biotic constraints, weed infestation has been found to be the most important biotic constraint with losses ranging from 30 to 100% depending on the locality (Balasubramanian *et al.*, 2007; Rodenburg and Johnson, 2009). The greatest yield losss due to weeds of 43% has been observed in Kenya (Diagne *et al.*, 2013). Diseases perceived to be of high relative importance include rice blast caused by the fungus *Magnaporthe grisea* (Skamnioti and Gurr, 2009), bacterial leaf blight, and rice yellow mottle virus (RYMV), while insect pests include stem borers and African rice gall midge (Seck *et al.*, 2010). Several abiotic factors remain a bottleneck to increasing rice productivity in SSA. These include drought, low soil fertility, salinity, alkalinity and deficiencies in soil macro-nutrients (Balasubramanian *et al.*, 2007; Diagne *et al.*, 2013). Of these, drought continues to prevail as the most important constraint limiting rice production and yield stability by smallholder farmers in rainfed upland and lowland ecologies in SSA (Seck *et al.*, 2010; Diagne *et al.*, 2013). Therefore to increase the yields of rice in the region, it is important to clearly identify through researcher – farmer interaction and collaboration what farmers preferred traits are and the production constraints they face.

Participatory plant breeding may be the better option towards achieving rice productivity in SSA, as it involves farmer participation. This method has been used successfully for faster release and widespread adoption of better adapted, more productive and acceptable varieties (Sperling *et al.*, 2001) in stress prone environments dominated by resource constrained small scale farmers (Bänziger and Cooper; 2001; Banziger and de Meyer, 2002). Through farmer – researcher collaboration, farmers and breeders interact to set breeding objectives and priorities (Sperling *et al*., 2001). Farmers provide information on their preferred cultivars (Sperling *et al*., 2001) and occurrence and relative importance of prevailing production constraints (Diagne *et al*., 2013). With this information the breeder can then fit the farmer desired plant into the target environment in terms of climatic and soil related factors, diseases and pest resistance (Derera *et al*., 2006). Participatory rural appraisal (PRA) tools are usually applied to determine farmers' perceptions and preferences (Morris and Bellon, 2004).

Although the cultivar traits commonly targeted in conventional breeding system include high yielding, early maturing, fertilizer responsiveness and dwarfness (Morris and Bellon, 2004), numerous PRA studies especially in SSA have revealed that rarely do the local farmers preferred plant ideotype correlate with that of scientists (Efisue *et al*., 2008). A PRA study in the Ashanti region of Ghana revealed that farmer's desired not only high yielding varieties but varieties that have specific grain quality attributes such as white coloured, long, slender and translucent grains (low chalkiness), fragrance and acceptable cooking quality (Asante *et al*., 2013). In Sikasso Region of Mali farmers in the upland and lowland rice ecologies preferred tall varieties and were willing to trade-off yield for grain quality and plant height (Efisue *et al*., 2008). In contrast, farmers in the irrigated ecology preferred high-yielding, long duration rice varieties (Efisue *et al*., 2008). According to Derera *et al*. (2006), small scale farmers can identify key production constraints prevailing in their local environments. For example, farmers growing maize in KwaZulu Natal province in South Africa prioritized stalk borers and cut worms as the most important insect pests while drought, excessive rains, hail storms and soil fertility prevailed as the most important abiotic stresses (Sibiya *et al*., 2013). A study conducted in marginal eastern belt of Zimbabwe indicated differences in prioritization of maize production constraints (Derera *et al*., 2006). Farmers in the high potential areas considered weevils as the most important, while drought was the most important for farmers in the less productive areas (Derera *et al*., 2006). More recently in Uganda, weeds and blast disease prevailed among the most important production constraints to finger millet (Owere *et al*., 2014). Therefore, to increase the chances of adoption of modern rice varieties especially in the marginal areas, it is imperative that farmers' priorities and needs are considered and incorporated in the breeding process. The objective of this study was therefore to investigate farmers' desired traits on rice cultivars and perceptions of production constraints in coastal region of Kenya.

2.2 Research Methodology

2.2.1 Description of the study area

The study was conducted in Msambweni Sub-county of Kwale County and Kaloleni sub-County of Kilifi County of coastal region of Kenya during 2013 and 2014. The study area covered two main agro- ecological zones suitable for rice production. The first is classified as the coastal lowlands sugarcane zone (coastal lowlands 2, CL2), occurring as a pocket in Ramisi area in Kwale county and is the wettest zone. This zone lies between 1 and 60 metres above seas level (masl), receives between 1,200 and 1,400 mm of rainfall annually and has a long to medium cropping season. The annual minimum and maximum temperatures in CL2 range from 14 to 32°C. The second zone is the coconut-cassava zone (coastal lowland 3, CL3), and occurs in both counties. This zone receives about 1,000 to 1,200 mm of rainfall annually and lies between 1 and 450 masl. The cropping season in CL3 is medium to long with intermediate rains in the first season and a very short second cropping season. The minimum and maximum annual temperatures in this zone vary from 17 to 32°C (Jaetzold and Schmidt, 1983). Soils of the coastal region are mainly sandy free draining soils. The soil fertility is generally low to very low because of the sandy topsoil and low organic matter. Nitrogen is a major limiting element in these soils as it is easily leached during heavy rains (Mureithi et al., 1995). The water holding capacity and cation exchange capacity (CEC) are extremely low, resulting in poor plant utilization of mineral fertilizers and hence low crop production. Moreover, in this study area, rice is produced in rainfed lowlands in the form of seasonally flooded and drought prone, coastal plains, valley bottoms, along the riverine and marshy lands. Although potential for rainfed upland ecology is enormous, rice breeding in this ecology has remained dormant until recently in 2010 when a few NERICA varieties were introduced. However, adoption of these varieties has been slow. Farmers have cited drought and lack of sufficient and sustainable seed supply as major drawbacks.

2.2.2 Sampling procedures

Country reports reveal that Kwale and Kilifi counties in coastal region of Kenya are the leading producers of rainfed rice (USAID, 2010). Bearing this in mind a predetermined sampling technique was used targeting in each county the sub-counties with the highest rainfed rice production. In collaboration with the ministry of Agriculture (MoA) extension officers, two sub-counties were selected namely, Msambweni in Kwale and Kaloleni in Kilifi county. In each sub-county four villages (Table 2.1) were identified. From each village at least one farmer who had great knowledge about the farms and local conditions was selected. These key informants assisted in identifying rice farmers for household survey and selecting focus group discussion sites.

2.2.3 Data collection

Data was collected from household survey using using structured questionnaire and from focus group discussions using semi structured questionnaire. Data collection was carried out by a team of eight members including the project manager, MOA extension officers from each sub-county and five trained enumerators. Prior to the time of survey, the team members including the eight key informants, one from each village convened for a brain storming session to review and improve on the questionnaires. Adjustments on the semi-structured questionnaire was done during this meeting while the structured questionnaire on household interviews was pretested on two farms in Mwagwei village in Msambweni sub-county and adjustments made accordingly. With guidance from the extension officers and the nodal farmers' focus group discussion sites and survey routes were mapped. The focus group discussions and the household interviews were administered concurrently. Farmers' involved in group discussions were not eligible for household interviews. This was done to avoid replication of information and to find out if there was an association between information obtained through focus group discussions and household interviews.

2.2.3.1 Focus group discussions

Focus group discussions were held in each village to obtain insights into the farmers' perceptions, needs, problems and rice management practices in an informal way. The discussion was guided in the local language and in *Kiswahili* using semi-structured questionnaire to keep the session on track while allowing respondents to talk freely and spontaneously. The technique employed consisted of problem listing, analyses and simple and pairwise ranking by the different groups. Notes were written down in English in note books and on flip chart. Farmers gave information on the rice production practices, rice varieties grown in each village, rice utilization, listed and ranked according to the most important constraints to rice production and preferred rice traits. Thereafter, a pair-wise ranking was conducted to compare the production constraints and preferred rice traits pair by pair. The scores were added and the mean calculated for ranking the rice production constraints and preferred cultivar traits. Overall a total of 102 farmers participated in the focus group discussions. Of the participating farmers', 70% were females (Table 2.1).

2.2.3.2 Household survey

The household interviews were administered using a structured questionnaire whereby the questions administered had been pre-selected. All the respondents were asked similar questions. Data were captured on the following themes; general background information, rice production and input use, varieties grown by farmers, rice traits preferred by farmers, production constraints, type of drought prevalent in each area, its causes and available mitigation strategies. Each individual farmer listed and ranked rice production constraints and cultivar attributes in order of importance. Overall a total of 224 farmers participated in the household survey. Of the participating farmers', 76% were females (Table 2.1).

Table 2.1: Number of farmers' interviewed in household survey and those who participated in focused group discussions in Msambweni and Kaloleni sub-counties of coastal lowlands of Kenya

		Focus groups		**Household survey**		
Sub-county	**Village**	**Male**	**Female**	**Male**	**Female**	**Total**
Msambweni	Mwagwei	3	11	7	20	41
	Bodo	0	18	4	25	47
	Ganda	8	6	10	20	44
	Bwiti	9	4	11	11	35
Kaloleni	Kizurini	0	9	4	26	39
	Garashi	2	10	3	24	39
	Vikindani	4	6	5	25	40
	Chilulu	5	7	3	26	41
Sub total		31	71	47	177	
Total		**102**		**224**		**326**

2.2.4 Data analysis

Statistical analyses were performed in SPSS (SPSS, Inc. Release 21 (2012)), computer package, and Genstat 14th edition (Payne *et al.*, 2011). Relationships were explored through percentages, mean comparisons and chi square values within and between sub-counties. The ranking of desired traits and production constraints was evaluated using the Kendall's coefficient of concordance (W) to identify the most important. The Kendall's coefficient of concordance (W) is a measure of degree of agreement/concordance among m set of n ranks. It is an index that measures the ratio of the observed variance of the sum of ranks to the maximum possible variance of sum of ranks. The essence of this index is to find the sum of the ranks for each attribute/factor being ranked and to examine the variability of this sum.

If the rankings are in perfect agreement the variability among these sums is said to be a minimum (Mattson, 1986). The analysis is a statistical technique that is used to identify and rank a given set of factors into the most pressing and then measures the degree of agreements among the judges. The identified factors are ranked according to the most pressing using numerals such as 1, 2, 3...,n, in that order. The factor with least total score is ranked as the most pressing, while the one with the highest score is ranked as least pressing. The computed total rank score is then used to calculate the W. The value of W is positive in sign and ranges from 0 to 1. It is 1 when the values assigned by one farmer are exactly the same as those assigned by other farmers, and is 0 when there is maximum disagreement among the farmers (Asante *et al.*, 2013).

2.3 Results

2.3.1 Household characteristics and crop management practices

The results from the formal survey showed that across the sub-counties, 43% of the respondents had no formal education with slightly more than 50% of the respondents being literate. Among the literate group only 10% had attained secondary education and above (Appendix 1). The main source of livelihood for most of the households interviewed was farming (83%) followed by off-farm self-employment (11%) and salaried employment (3%).

The actual average area under rice production per farmer was approximately 0.3 ha while on average each farmer owned approximately 0.6 ha of underutilized land for expansion of rice production in the region (Appendix 2). The main planting season was the long rain season from March to August with only a few farmers planting during the short rain season from October to December. The main cropping practice was monocropping. Sources of seed for planting were recycled seed from previous season (55%), market (24%) and exchanged with the other farmers (16%). Only a few farmers (10%) had received seed from the MOA which was mainly seed of the introduced NERICA varieties (Appendix 2). Results from the focus group discussions were also in agreement with the formal survey regarding the main source of seed (Appendix 4) which was their own stock. The second option was either market or exchange with other farmers. However, farmers from Bodo and Ganda village in Msambweni deviated from the norm in that they had to buy planting seed from the market. They pointed out that rice was their main staple food and all the harvest was consumed with hardly anything left to store as seed for next planting season.

Method of land preparation differed between counties with manual labour being the most common (64%), followed by oxen plough (26%) and the use of tractor was the least popular

(10%). The use of tractor was mainly in Msambweni (16%) (Appendix 2). Likewise, during focus group discussions farmers in all the eight villages indicated manual labour as the main land preparation method (Appendix 4). Ox-plough was embraced by a few farmers in Mwagwei, Ganda and Bwiti, while preparation of land using tractor was only in Mwagwei village in Msambweni.

Results from formal survey on the percentage of farmers practicing different agronomic practices are presented in Appendix 3. The majority of the farmers sowed their seed directly just before the beginning of the rains with only a few (2.8%) farmers in Msambweni sowing seed in nurseries for transplanting. In Msambweni, broadcasting was the most popular planting method (93%) while row planting (51%) and dibbling (47%) were the most popular improved technologies in Kaloleni. The majority of the farmers (98%) did not use fertilizer with only 2% embracing the practice. The use of organic manure was also very low and was used by less than 10% of the farmers. Differential weeding times were observed between the counties. In Msambweni 65% of the farmers weeded thrice while in Kaloleni 70% of the farmers weeded twice. The first weeding was done using hoes while the second and third weeding were mainly hand picking. Rice harvesting was predominantly done by cutting individual panicles with a knife or by hand. Harvesting using sickles was attempted by a small percentage of the participating farmers. These findings were supported by results from focus group discussions (Appendix 4) that the most common agronomic practices were use of manual labour, direct seeding, broadcasting in Msambweni and dibbling in Kaloleni. The use of inorganic fertilizer was not popular among farmers while organic manure was used by a few farmers in in Bodo and Ganda villages in Msambweni and Kizurini village. Overall on gender, the results revealed that rice was a woman’s crop with majority of the women being involved in land preparation (66%), planting (73%), and weeding (71%). Although all members were involved in harvesting, still women dominated in this activity.

2.3.2 Rice varieties grown by farmers and usage

The majority of the farmers had grown local varieties for a period of not less than 30 years. At least 24 landraces, two old improved and two modern varieties were grown in the region (Appendix 5). Of these, the most popular landrace in Msambweni was Kitumbo whereas Sigaye dominated in Kaloleni (Table 2.2). The variety Ambale was grown across the sub-counties by 64% of the participating farmers. The variety Supaa was the most popular old improved variety in Msambweni and was grown by at least 70% of the participating farmers. Pishori, an old improved variety was grown by 21% of the farmers across the Sub-counties. Sigaye and Supaa are tall, late maturing varieties characterized by white, long, fat, and aromatic grains, big panicles, and few tillers. Farmers mentioned that these varieties had a high demand for water and nutrients and succumbed to water stress especially if drought occurred during the flowering stage. On the contrary, Kitumbo was somehow drought tolerant, medium maturing with short, bold, white grains. Pishori was a low yielding aromatic and old improved variety with long, white and slender grains. This variety was grown mainly for confectionery purposes. The introduced NERICA 4 was grown by 14% of the farmers in Kaloleni and only 1% in Msambweni.

Table 2.2: Common rice varieties mentioned and percentage of farmers growing them in Msambweni and Kaloleni sub-counties

Variety	**Sub-Counties**		**Type**
	Msambweni	**Kaloleni**	
Ambale	41.5	84.6	Landrace
Sigaye	0.0	100.0	Landrace
Kitumbo	82.4	0.0	Landrace
Madevu	75.7	0.0	Landrace
Kibawa cha nzi	6.1	5.3	Landrace
Niwahi	18.2	0.0	Landrace
Pishori	25.3	16.2	Old improved
Supaa (Pachaga)	69.7	0.0	Old improved
NERICA	0.9	13.6	Modern improved

Among the respondents interviewed rice was an important staple food crop, more important than maize. All the participating farmers indicated that they grew rice mainly for home consumption. Of the produce, 70% was mainly for home consumption while 20% was sold to brokers or directly in the market. Milled rice for home consumption was cooked by boiling, making special coastal rice dishes such as *pilau, and biryan*. Other minor uses were baby weaning, given as a gift and donations to family ceremonies. Use of rice culms as animal feed was not mentioned among the participating respondents. Once harvested the culms were left in the farm and incorporated in the soil during the next planting season.

2.3.3 Speciality rice varieties and usage

Of the participating farmers in the formal survey, 86% in Msambweni and 18% in Kaloleni grew different rice varieties for bread making and other confectionery purposes (Table 2.3). Across sub-counties, Pishori an old improved variety was the most popular. This was followed by Madevu and Niwahi in Msambweni and Sigaye in Kaloleni. The criterion given by farmers for identifying and selecting suitable varieties for bread making were white milled rice flour with low fat content, the dough should be easy to work on, absorbs little water, swells, rises up, became porous and does not stick on the baking tin while baking. Taste and aroma were not mentioned among the qualities for identifying varieties for bread making.

Table 2.3: Speciality rice varieties mentioned and percentage of farmers growing them in Msambweni and Kaloleni sub-counties

Variety	**Sub-county**		**Overall**
	Msambweni	**Kaloleni**	
Pishori	33.3	10.3	21.4
Madevu	15.7	0.0	7.6
Niwahi	13.9	0.0	6.7
Kivunga	8.3	0.0	4.0
Sigaye	0.0	5.2	2.7
Kibawa cha inzi	2.8	1.7	2.2
Ringa	3.7	0.0	1.8
Kimachomacho	2.8	0.0	1.3
Supaa	2.8	0.0	1.3
Manyoya	1.9	0.0	0.9
Ambari	0.0	0.9	0.4
Riziki	0.9	0.0	0.4
Overall	**86.1**	**18.1**	**50.9**

Farmers indicated that these were not important because more ingredients were added to the flour to make the rice bread tastier. Other rice confectionary products made by the farmers were *vitumbua, Kibibi*, and *Matobosho.* For these products soft and porous dough is not a requirement and therefore they are made using flour from any rice variety.

2.3.4 Preferred rice characteristics

Results from the formal survey showed that there were significant differences in farmers' preferences for rice traits between the counties since the computed chi-squared value was larger than the corresponding tabular value with 17 degrees of freedom at 0.05 and 0.01 level of significance (Table 2.4). Although differences existed among farmers in their preferences for rice traits, ranking of the first seven traits was comparable at county level and across. All participating farmers' considered high yield potential as the most important trait. This was followed by drought tolerance, bird resistance, short duration, aroma, weed competition and high tillering ability, in that rank order. In Kaloleni County, importance of drought tolerance and bird resistance was comparable to that of high yield potential. Apart from the seven most important traits mentioned above, preference for the other traits differed among counties. For grain quality traits, long fat grains was more important than taste and white grain colour in Msambweni, while in Kaloleni the latter was more important. Besides baking qualities were significant to 66% of the farmers in Msambweni compared to 22% in Kaloleni. Medium plant height was of concern to two thirds of the respondents in Kaloleni and only slightly less than half in Msambweni. Tall and short plant height, medium and long

Table 2.4: Desired traits indicated by farmers during the formal survey at and across Msambweni and Kaloleni sub-counties (% of farmers selecting a trait and ranking)

	Sub-counties				**Across**	
	Msambweni		**Kaloleni**			
Traits	**%**	**Rank**	**%**	**Rank**	**%**	**Rank**
High yield potential	100.0	1	100.0	1	100.0	1
Drought tolerant	96.3	2	100.0	1	98.2	2
Resistance to bird damage	95.4	3	100.0	1	97.8	3
Short duration	92.6	4	94.8	2	93.8	4
Aroma	91.7	5	91.4	3	91.5	5
Weed competition	76.9	6	86.2	4	81.7	6
High number of tillers	73.1	7	79.3	5	76.3	7
Taste	68.5	9	67.2	8	67.9	8
White grain colour	60.2	11	75.9	6	67.4	9
Long and bold	71.3	8	57.8	9	64.3	10
Medium plant height	46.3	12	71.6	7	59.4	11
Baking qualities	66.7	10	22.4	11	43.8	12
tolerant to low soil fertility	34.3	13	39.7	10	37.1	13
Tall plant height	27.8	14	3.4	13	15.2	14
Short plant height	5.6	15	7.8	12	6.7	15
Medium duration	1.9	16	0.9	14	1.3	16
Long duration	1.9	17	0.0	16	0.9	17
Feed for livestock	0.0	18	0.9	15	0.4	18

Chi-square computed value =61.82 and tabulated values with 17 d.f, at the 0.05 and 0.01 level of significance is 27.59 and 33.41

duration, and feed for livestock were of concern by less than 16% of the respondents and therefore considered the least preferred traits.

Results from the focus group discussions indicated that across the counties, the Kendall's W of 0.754 was significant at 1% level suggesting that 75% of the farmers agreed on the outcome of the ranking (Table 2.5). The highest agreement among households was observed in Kwale (85%) followed by Kilifi (78%). Overall, high yield potential was the most important desired trait. Preferences for drought tolerance and short duration were ranked similarly as the second most important traits. High tiller number, and tasty and aroma were ranked third while medium plant height was fourth in ranking. Surprisingly, although resistance to bird damage was the third most important trait mentioned during the formal survey, it did not feature among the most important traits during the focus group discussions.Baking qualities were viewed as moderate and least important in Msambweni and Kaloleni, respectively. This agreed with the results obtained from the formal survey where baking qualities were more important in Msambweni than in Kaloleni County.

Table 2.5: Ranking from scores of pairwise ranking of the traits desired by the farmers during focus group discussions

Traits	**Msambweni**		**Kaloleni**		**Overall**	
	Mean rank	**Rank**	**Mean rank**	**Rank**	**Mean rank**	**Rank**
High yields	1	1	1.5	1	1.2	1
Short duration	2.6	2	2.8	2	2.7	2
Drought tolerant	3.8	3	2.9	2	3.3	2
High tiller number	5.4	5	4.5	3	4.9	3
Tasty and aroma	4.2	4	6.4	4	5.3	3
Medium plant height	5.2	5	6.9	5	6.1	4
Long and bold	7.5	6	9.0	7	8.2	5
Resistant to pests and diseases	8.4	7	8.1	6	8.2	5
Heavy panicles	9.6	8	7.0	5	8.3	6
Low input use	11.1	10	8.8	7	9.9	7
Resistance to bird damage	10.8	9	11.5	9	11.1	8
Good Shattering	12.9	11	9.9	8	11.4	8
Baking Qualities	9.5	8	14.0	10	11.8	9
Weed competitor	13	12	11.9	9	12.4	9
Kendall's W (Significance)	**0.845 (0.001)**		**0.783 (0.001)**		**0.754 (0.001)**	

2.3.5 Production constraints

Results from the formal survey showed that the computed chi square value for production constraints in the two counties was smaller than the corresponding tabular value with 15 degrees of freedom at 5% and 1% level of significance (Table 2.6). This indicated that production constraints experienced by farmers were comparable between sub-counties. Across sub-counties, there was consistency in ranking of the five most important constraints. Farmers ranked drought and poor distribution of rainfall as the most important. This was followed by pests mainly stem borers and diseases, unavailability of certified seed, damage

Table 2.6: Rice production constraints during formal survey at and across Msambweni and Kaloleni sub-counties

Production constraint	**Msambweni (n=108)**		**Kaloleni (n=116)**		**Across**	
	%	**Rank**	**%**	**Rank**	**%**	**Rank**
Drought (June winds) and poor rainfall distribution	97.2	1	99.6	1	98.5	1
Pests (e.g stem borers) and diseases	88.9	2	98.3	2	93.8	2
Lack of improved cultivars and Unavailability of certified seeds	88.0	3	87.9	3	87.9	3
Damage by birds	81.5	4	78.5	4	80.0	4
Inadequate extension services	73.1	5	75.9	5	74.6	5
Limited technology knowhow on recommended agronomic practices	73.1	5	69.0	7	71.0	6
Lack of access to inputs	65.7	6	71.6	6	68.6	7
High cost of inputs	59.3	7	65.5	8	62.5	8
Lack of irrigation	54.6	8	61.2	9	57.8	9
Low yielding varieties	37.0	10	55.2	10	46.4	10
Lack of market	38.9	9	34.5	12	45.5	11
Low soil fertility	25.0	13	41.4	11	33.5	12
Lack of labour	27.8	11	27.6	13	27.7	13
Low paddy price	26.9	12	25.0	14	25.9	14
Salinity	13.0	14	20.7	15	17.0	15

Chi-square computed value =10.25 and tabulated values with 14d.f, at the 0.05 and 0.01 level of significance is 23.58 and 29.14

by birds and inadequate extension services in that rank order. In Msambweni, inadequate extension services and limited technology know-how were ranked similarly by 73% of the farmers while in Kaloleni lack of access to inputs was more important that limited technologyand know-how. Salinity, low paddy price, lack of labour and in Msambweni low soil fertility were identified as the least important since they were of concern to less than a third of the participating farmers.

Results from the focus group discussions indicated that across the counties, the Kendall's W of 0.758 was significant at 1% level suggesting that 76% of the farmers agree on the outcome of the ranking (Table 2.7). The highest agreement among households was observed in Kaloleni (85%) followed by Msambweni (78%). At and across the sub-counties, there was consistency in ranking of the first four most important constraints. Although the ranking slightly contradicted that observed in formal survey, drought and poor rainfall distribution was ranked as the most important. This was followed by non-availability of seeds, pests and diseases and limited know-how on agronomic technologies. At and across sub-counties, farmers ranked high cost of fertilizer inputs, slow harvesting technique and exploitation by brokers similarly at position 7, 9 and 10 respectively. Msambweni farmers

Table 2.7: Ranking from scores of pairwise ranking of perceived production constraints during focus group discussions at and across Msambweni and Kaloleni sub- counties

Production constraints	**Msambweni (n=59)**		**Kaloleni (n=43)**		**Overall**	
	Mean rank	**Rank**	**Mean rank**	**Rank**	**Mean rank**	**Rank**
Drought (June winds)and poor rainfall distribution	1.4	1	1.2	1	1.3	1
Non-availability of seed	2.6	2	2.0	2	2.3	2
Pests and diseases including weeds	2.9	3	3.1	3	3.0	3
Limited technology knowhow on recommended agronomic practices	3.4	4	4.6	4	4.0	4
Damage by birds	6.9	6	5.8	5	6.3	5
Inadequate extension services	5.9	5	7.8	8	6.8	6
High cost of fertilizer inputs	7.8	7	6.8	7	7.2	7
Low soil fertility	9.2	11	6.2	6	7.8	8
Slow harvesting technique	8.6	9	8.0	9	8.3	9
Exploitation by brokers	9.0	10	9.8	10	9.4	10
Damage by wild pigs	8.4	8	10.8	11	9.6	11
Kendall's W (Significance)	0.776 (0.001)		0.846 (0.001)		0.758 (0.001)	

ranked low soil fertility as the least important and this agreed with the outcome of the formal survey. In Kaloleni damage by wild animals was the least important however, this was not mentioned as a constraint during the formal survey.

2.3.6 Drought patterns in rice

Farmers experienced different levels of drought stress at different growth stages of the rice crop (Table 2.8). At seedling stage 27% of the farmers experienced mild stress in their farms while 63% indicated that drought was not a problem. Vegetative drought stress was characterised as severe by 38% and not a problem by 44% of the farmers. The levels of drought stress during flowering to grain filling were characterized as severe to very severe by over 80% of the farmers. This clearly indicated in Kwale and Kilifi counties of lowland coastal Kenya, drought stress occurring at reproductive and grain filling stage was the most important. Poor distribution of rainfall was considered as a major cause of drought stress occurring at all the growth stages of rice. Drought caused by June winds was a major cause of water stress at both reproductive and grain filling growth stages. At all growth stages nearly all the farmers did not attempt to mitigate the effects of drought.

Table 2.8: Overall percentage of farmers experiencing different levels of drought and causes at different growth stages of rice in Msambweni and Kaloleni sub-counties

	Percentage of farmers			
Stage of rice growth	**Seedling**	**Vegetative**	**Reproductive**	**Grainfilling**
Severity of drought				
Mild	27.0	16.4	11.6	2.7
Severe	9.4	37.4	38.8	37.8
Very severe	0.5	2.3	45.1	51.7
Not a problem	63.2	43.9	4.6	7.7
Causes				
Delayed planting	3.7	0.0	0.0	0.0
Poor distribution of rainfall	38.8	56.4	53.6	44.2
Drought including June winds	0.0	0.9	41.7	55.8

2.4 Discussion

2.4.1 Household characteristics and crop management practices

In coastal lowlands of Kenya, rainfed rice production was predominantly a women's affair. Wekesa *et al*. (2003), also reported that in the coastal lowlands of Kenya, women are responsible for producing food crops, while men tend to be responsible for growing and marketing tree crops. Elsewhere in Sikasso region of Mali, Efisue *et al*. (2008) reported that rice was perceived as a women's crop especially in the lowland and irrigated rice ecologies. These findings imply that more women than men should be involved in designing breeding and agronomic rice technologies. This will highly impact on adoption of the finished products. The PRA also established that rice and not maize was the principal crop in the eight villages of Msambweni and Kaloleni sub-counties. The farmers grew rice mainly for subsistence with the surplus being stored as seed or sold to finance other family needs. The average potential area for rice production per farmer was approximately 0.6 ha indicating that there was ample land for expansion of rainfed rice production in the region. The majority of the farmers managed their rice farms using manual labour. Mechanization will be necessary to allow substantial increases in farm size.

The growing season for rice extends from mid-March till late August, which implied that double cropping is possible. Options for double cropping include, availing early to medium maturing varieties, transplanting the second crop or possibly ratooning the first crop. Farmers in Msambweni predominantly broadcasted their rice seed during planting. They believed that the method was less labour intensive, time consuming and tiresome. However, they admitted that with this method, quantity of seed used for planting was high. On average, seeding rate was 100 kg per hectare compared to the recommended seed rate of 25 kg per hectare. In contrast, majority of farmers in Kaloleni had embraced row planting and dibbling as a way of planting. The average seeding rate was about 60 kg per hectare which was twice above the recommended rate. A close examination revealed that most of the farmers in Kaloleni had embraced these technologies from the Ministry of Agriculture extension services. Information dissemination should therefore be strengthened in order to move rice production from deficit to surplus in the region.

The majority of the farmers did not apply fertilizer to their rice fields. The perception that rice was like a grass and therefore has the capacity to sustain itself under natural conditions; that their soils had adequate fertility, and lack of knowledge on how to apply the fertilizer were among reasons farmers gave for not applying fertilizer. Results from a survey on adoption of maize production technologies in coastal lowlands of Kenya revealed that adoption of new technologies especially for fertilizer has remained low, due to similar beliefs (Wekesa et al., 2003). Farmers admitted that over the years soil fertility has deteriorated in the region partly due to monocropping, cultivation on the same pieces of land without replenishment of the nutrients and more recently severe floods caused by climate change washing out vital nutrients and sediments to the ocean. Development of rice varieties with high use of nitrogen, phosphorous and other nutrients efficiently cannot be overemphasized.

The common harvesting method was cutting individual panicles with a knife or by hand. Ease of harvesting, transportation, storage, threshing and uneven maturity of the tillers and the crop on whole were mentioned as some of the reasons why farmers use the practice. With this method farmers admitted that it was slow and could take about 75 days harvesting one hectare. Broadcasting and overreliance on landraces and out-dated varieties contribute to uneven maturity of the crop. This increases labour for bird scaring and any delay in harvesting culminates to low yields. Therefore, in this region and other regions in sub-Saharan Africa where farmers have continued to use traditional technologies there is an opportunity to increase rice production, through introduction of modern harvesting technologies and varieties with uniform maturity.

2.4.2 Rice varieties

Although rice cultivation was introduced in the coastal region in 1907 (Kouko, 1997), little progress has been made in breeding to address the farmers' needs. This was substantiated by the fact that majority of the farmers in the region were growing their local landraces. These landraces were identified with different names, differed in phenotype and were adapted to the local environment. Kitumbo and Sigaye were the most common landraces grown by over 80% of the participating farmers in Msambweni and Kaloleni, respectively. Farmers' high preference for their landraces suggested that breeders would make impact by improving or breeding from these cultivars because they are already adapted to the local environment. Improvements would target reducing plant height, incorporating drought tolerance traits and a shorter maturity period, so that they can be grown twice in the long rain season and during the short rain season. Moreover for Kitumbo, aroma and traits that confer baking quality will need to be improved in collaboration with the farmers.

2.4.3 Preferred traits in rice varieties

Results indicated that majority of the farmers (>90%) preferred high yielding, short duration cultivars with tolerance to drought stress. The reasons for short duration cultivars (less than 110 days to maturity) with tolerance to drought stress is that over the years farmers have observed that since their local varieties were long duration (140-160 days to maturity) the effects of June winds on rainfall coincided with the critical stages of development resulting in low grain yields. Moreover, farmers were not growing rice during the short rain season (October to December) because none of the farmers' varieties could fit in this season. Preference for short duration varieties means that farmers may plant two rice crops in the long rain season by, transplanting the second crop or possibly ratooning the first crop and one crop in the short rain season thus increasing rice production in the region. On plant height; farmers preferred medium plant height because of ease of harvest and reduced lodging which occurs in taller plants. According to Kimani *et al*. (2011) very short varieties are usually near the ground and would increase damage due to rodents, water splash, ground walking birds and termite damage on grains. In addition, birds found it easy to perch on the shorter varieties because they have relatively stronger culms.

Of the subjective traits farmers preferred aroma, taste, white, long and bold grains. It was observed that preference of the two old improved varieties (Supaa and Pishori) grown in the region was mainly due to their taste and aroma and for Supaa long and bold grains. One of the unique preferences by nearly 50% of farmers was cultivars with good baking qualities. Important traits for a variety with good baking qualities were white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin upon baking. The reason why farmers treasured varieties with these qualities was that rice as mentioned earlier was a major staple food among the participating communities and diversity of the varieties allowed the crop to have many uses. Rice bread was one of the cultural rice products common in most traditional ceremonies. For school going children it was cheap and convenient for breakfast and the farmer could save on the limited financial resources. This emphasizes the importance of breeding multipurpose cultivars combining high grain yield, earliness and drought tolerance, medium height, good culinary and baking qualities. The culinary and baking traits are a function of human perceptions and are difficult to measure quantitatively (Morris and Bellon, 2004). Therefore identification and evaluation of these traits will require close collaboration between the local breeders and farmers'.

2.4.4 Production constraints

Drought and uneven distribution of rainfall were ranked as the major constraints to rice production in coastal region. This confirms finding made by Muti and Kibe (2009), that the coastal region of Kenya is characterised by frequent droughts which occur in succession of two to three years. In other regions of SSA drought has also been reported to be the most important climatic related constraint to rice production in the rainfed upland and lowland ecologies (Diagne *et al*., 2013). Rice yield losses due to drought of up to more than 40%

have been reported in Gambia, Senegal and Côte d'Ivoire (Diagne *et al.*, 2013). The major biotic stresses reported by the majority of the farmers were stem borers. The most common stem borer species often seen in the farmers' fields were the *Chilo polychrysus* (dark headed). Other species that have been identified in the coastal region include *Chilo partellus, Sesamia calamistis* and *Maliarpha separatella* (Ho, 1984). A close examination in the farmers' fields showed that incidence and severity of these insects has increased possibly due to effects of climatic change. The severity of these pests coincided with periods of drought prompting farmers to confuse their damage with that from drought stress. Farmers did not apply any form of control mainly due to lack of capital. Stem borers damage the rice crop at all growth stages by feeding upon tillers, causing dead heart or drying of the central tiller during the vegetative stage, and causing whiteheads at reproductive stage. A literature survey did not find any quantification of crop losses caused by these important insect pests in the coast region.

Unavailability of certified seeds, lack of technology know-how on agronomic practices and inadequate extension services were mentioned as the major socio-economic production constraints. Unavailability of seed is a major problem to rice production in the region and continues to reduce the actual area under rice production. Majority of the farmers recycle their own seeds. Those who consume all the produce have to buy from the market. The market price ranges from USD 1.2 to 2.5 per kg of which about USD 200 is required to buy enough seed for a hectare and most farmers could not afford. This results in substitution of the rice farms with other crops or they are left bare until the next season. Seed for the newly released NERICA varieties is never enough and has to be sourced from Mwea, another rice growing region in Kenya, creating geographical inconveniences. Establishment of community based seed systems is therefore advocated. Lack of capital and information on the proper agronomic practices contribute to continued use of traditional methods of crop management such as broadcasting, failure to apply fertilizer and lack of control of pests and diseases. This has also resulted in farmers growing their traditional and obsolete varieties with low yields due to lack of options. The role of extension staff in disseminating the recommended agronomic practices was evident in Kaloleni where about half of the participating farmers had embraced row planting technology. Therefore, strengthening information dissemination on proper agronomic practices and new technologies will involve breeding in partnership with agronomists, farmers and government extension.

2.4.5 Patterns of drought in rice

Farmers' knowledge and experience is the most accurate and simplest approach for characterization of drought patterns prevalent in a region (Fischer *et al.*, 2003). As stated earlier the main rice growing season in this region is the long rain season from March to August. Different drought patterns develop during the growing season. Farmers indicated they experienced minor drought stress during seedling and vegetative stage. In contrast, drought in the region was more pronounced during the reproductive and grain filling stages of the rice crop significantly affecting rice productivity. Farmers were quick to mention that the major cause of water stress during the reproductive stage was what was locally termed as "*Upepo Mkali"* or *"June winds*" emanating from the Indian Ocean which occurs between May and June. These winds chase away rain bringing abrupt drought conditions in the middle of the long rain season (Muti and Ng'etich, 2009). Farmers mentioned that the main effects of these winds on the rice crop were the presence of white heads, increased spikelet infertility because most of the spikelet opens up and the pollen is blown off before pollination, premature grain development, lodging, and increased incidences of pests and diseases mainly stem borers and the brown spot disease. These findings were in agreement with reports by Muti and Kibe (2009), that although the coastal lowland of Kenya is endowed with enormous agricultural potential of good soils and annual average rainfall and that the long rain season is the most reliable, there appears to be a unique climatic phenomenon locally termed "*June winds*" caused by the east African low level jet stream. They observed during the La Niño years when June winds were prominent, that average maize yield was 0.9 t ha^{-1}, while during El Niño years when June winds appeared suppressed or diverted from the region, average maize yields of 4.1 t ha^{-1} were realized. Effects of drought on rice yields during the La Niño and El Niño years in the coastal region are yet to be quantified.

2.5 Conclusions, implications for breeding and recommendations

The results of this study showed that rice was the major food crop in the eight villages of Msambweni and Kaloleni sub-counties. Rice production was subsistence oriented and dominated by women farmers implying that more women than men should be involved in designing breeding and agronomic rice technologies. This will highly impact on adoption of the finished products. The majority of the farmers managed their rice farms using manual labour and did not apply fertilizer to their rice fields. Policies and programmes that encourage mechanization and fertilizer use will be necessary to allow substantial increases in farm size and rice productivity in the region.

The study found that the majority of the farmers grew local landraces. Farmers treasured these varieties because of their culinary and baking qualities. Breeders would therefore make an impact by improving through breeding these cultivars because they are already adapted to the local environment. For a new cultivar in the region, farmers would prefer it to have high grain yield, early maturity, drought tolerance and medium height. For subjective traits farmers preferred aromatic, tasty, white, long and bold grains. Important traits for a variety with good baking qualities were white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin upon baking. On production constraints, drought, pests and diseases were ranked as the most important. Drought was common at reproductive and grain filling stages suggesting the need to breed for drought tolerance at these stages. In conclusion, participatory breeding will be necessary to fit the farmer desired plant into the target environment in terms of climatic related factors, diseases and pest resistance.

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Appendices

Appendix 1: Household characteristics of participating farmers during the formal survey in Msambweni and Kaloleni sub-counties of coastal lowlands of Kenya

Characteristics	Kwale (n=116)	Kilifi (n=108)	Overall (N=224)
Education			
No formal education	43.5	43.1	43.3
Primary	45.4	48.3	46.9
Secondary (Ordinary level)	5.6	6.0	5.8
Secondary (Advanced level)	3.7	1.7	2.7
Tertiary	1.9	0.9	1.3
Main Occupation			
Farming	80.6	84.5	82.6
Salaried employment	2.8	2.6	2.7
Self-employment off-farm	13.0	8.6	10.7
Off-farm worker	2.8	0.0	1.3
Casual	0.0	3.4	1.8
House keeping	0.0	0.9	0.4
Others	0.9	0.0	0.4

Appendix 2: Mean values for area under rice production and % of farmers indicating main cropping system, land preparation method and fertilizer use during formal survey in Msambweni and Kaloleni sub-Counties

Parameter	Sub-County Msambweni (n=108)	 Kaloleni (n=116)	Overall
Area (Hectares)			
Average actual area	0.4	0.2	0.3
Average potential area	0.8	0.4	0.6
Season and month of planting			
Long rains	100.0	100.0	100.0
Short rains	2.8	8.6	5.7
Main cropping system			
Monocropping	92.6	94.8	93.7
Intercropping	0.0	0.0	0.0
Source of seed			
Own	54.6	55.2	54.9
Exchange with other farmers	14.8	19.0	16.9
Market	30.6	19.8	25.2
MOA	0.0	1.7	0.9
Method of land preparation			
Manual Labour	43.5	84.5	64.0
Ox-plough	39.8	12.1	25.9
Tractor	16.7	3.4	10.1
Gender involved in land preparation			
Male	23.1	6.0	14.6
Female	53.7	78.4	66.1
Both	**22.2**	**14.7**	**18.4**

Appendix 3: Percentage of farmers practicing different agronomic practices and gender involved during formal survey in Msambweni and Kaloleni sub-Counties

Agronomic practice	**Sub-County**		**Overall**
	Msambweni (n=108)	**Kaloleni (n=116)**	
Planting			
Sowing method			
Direct seeding	97.2	100.0	98.6
Transplanting	2.8	0.0	1.4
Planting method			
Row planting	7.4	50.9	29.1
Broadcasting	92.6	1.7	47.2
Dibbling	0.0	47.4	23.7
Gender involved in planting			
Male	9.3	1.7	5.5
Female	63.0	82.8	72.9
Both	25.0	13.8	19.4
All members including children	1.9	1.7	1.8
Fertilizer application			
Inorganic			
Use	0.0	3.4	1.7
Do not use	100.0	96.6	98.3
Organic			
Use	0.9	10.3	5.6
Do not use	99.1	89.7	94.4
Weeding			
Number of times			
None	0.0	0.0	0.0
Once	1.9	4.3	3.1
Twice	30.6	69.8	50.2
Thrice	64.8	25.0	44.9
Gender involved in weeding			0.0
Male	7.4	0.0	3.7
Female	61.1	79.3	70.2
Both	26.9	18.1	22.5
All members including children	3.7	0.9	2.3
Harvesting			
Harvesting method			
Cutting stems with a sickle	5.6	1.7	3.6
cutting individual panicles	93.5	98.3	95.9
Gender involved in Harvesting			
Male	10.2	0.9	5.5
Female	62.0	63.8	62.9
Both	25.9	18.1	22.0
All members including children	**1.9**	**17.2**	**9.5**

Appendix 4: Some agronomic practices indicated by farmers during focus group discussion in the selected villages in Msambweni and Kaloleni sub-Counties

Sub-Counties	**Msambweni (n=59)**				**Kaloleni (n=43)**			
Villages	**Mwagwei**	**Bodo**	**Ganda**	**Bwiti**	**Kizurini**	**Garashi**	**Vikindani**	**Chilulu**
Season of planting								
Long rain	√	√	√	√	√	√	√	√
Short rain								
Source of seed								
Own stock	√			√	√	√	√	√
Exchange with other farmers				√			√	√
Market	√	√	√		√	√		
Land preparation								
Manual labour	√	√	√	√	√	√	√	√
Ox- plough	√		√	√				
Tractor	√							
Planting								
Sowing method								
Direct seeding	√	√	√	√	√	√	√	√
Transplanting								
Planting method								
row planting			√					
Broadcasting	√	√	√	√				
Dibbling					√	√	√	√
Fertilizer use								
Inorganic								
Use								
Do not use	√	√	√	√	√	√	√	√
Organic								
Use		√	√		√			
Do not use	√	√	√	√	√	√	√	√
Weeding								
Number of times								
None								
Once								
Twice	√	√	√	√	√	√	√	√

Appendix 5: Rice varieties grown by farmers in Msambweni and Kaloleni sub-counties in coastal lowlands of Kenya

Varieties			
Local landraces		Old Improved	Modern
Ambale	Makonde	Pishori	NERICA 4
Sigaye	Mivi ya Kibiriti	Supaa(Pachaga)	NERICA 1
Kitumbo	Mchonyi		
Kibawa cha nzi	Mundindiko		
Niwahi	Kaniki		
Madevu	Kijengo		
Manyoya	Subiri Mwana		
Ringa	Mwarabu		
Mchecheka	Gushe		
Katele	Shingo la Mjakazi		
Kapura Fimbo	Gomba		
Moshi	Bibi wa Mwaka		

Chapter Three

Variability of rice genotypes during reproductive stage under drought and no-drought conditions

Abstract

Grain yield of rice is reduced when drought stress occurs during the reproductive growth stage. The objective of this study was to determine genetic variability for drought tolerance among 21 rice genotypes comprising of 6 interspecific and 15 *O. Sativa* genotypes. Due to differences in maturity two experiments were set up at Kenya Agricultural and Livestock Research Organization (KALRO) - Mtwapa between April 2013 and March 2014. The first experiment consisted of 15 medium to late maturing genotypes evaluated in a steel and wire mesh screen house where weather conditions were uncontrolled. The second group consisted of six early maturing rice genotypes evaluated in an open field. Both experiments received similar treatments of no drought and drought conditions during the reproductive growth stage. Plants were planted in black polythene pots arranged in a randomized complete block design with four replications. Data collection included canopy temperature, relative leaf water content, leaf rolling and drying, days to 50% flowering, spikelet fertility and grain yield per plant. The study revealed that there were no significant differences among rice genotypes for all the physiological traits measured under no drought conditions. However, under drought conditions, genotypes varied significantly ($P \leq 0.001$) for all the physiological traits and in days to 50% flowering, spikelet fertility and grain yield per plant. The drought tolerance index was useful in determining the effect of drought stress on each genotype and showed that among the medium to late maturing genotypes drought stress caused relative reduction in, grain yield per plant (57%), spikelet fertility (37%), relative leaf water content (34%) and relative increase in canopy temperature (19%). The mean leaf rolling and drying scores were 6 and 3, respectively while average delay in flowering was eight days. Two local cultivars, Shingo la Mjakazi and Kitumbo were moderately drought tolerant while genotypes NERICA-L-25, Tuliani and Kibawa Chekundu were highly drought susceptible. The local cultivars Tuliani and Supaa were potential donors for high number of grains per panicle and heavy grains. Among the early maturing group, drought stress caused relative reduction in spikelet fertility of 34% with mean leaf rolling score of 4 and delay in flowering of five days. Selection index effectively identified drought tolerant and susceptible genotypes. The genotype CT16323-CA-25-M was highly drought tolerant, NERICA 2 was moderately tolerant and CT16333(1)CA-22-M was drought susceptible. In both experiments, spikelet fertility was correlated with grain yield and the other physiological traits under stress. Breeders may use spikelet fertility to indirectly select for grain yield under drought conditions.

Key words: Drought tolerance, drought tolerance index, genotypes, selection index, spikelet fertility, rice

3.1 Introduction

Rice production and productivity in sub-Saharan Africa (SSA) is limited partly by abiotic and biotic factors which vary significantly across growing environments and countries. Among the abiotic constraints, drought continues to prevail as the most important constraint limiting rice production and yield stability by smallholder farmers in rainfed upland and lowland ecologies in SSA (Seck *et al.*, 2010; Diagne *et al.*, 2013). Currently, the available cultural practices for drought mitigation during the early stages of rice growth and development usually result in a drop in the rice yields (Pandey *et al.*, 2007). When drought occurs late in the season, for example, during flowering or grain filling stage, flexibility in making management adjustment is limited resulting in drastic yield reduction and may even lead to total crop failures (Pandey *et al.*, 2007). Although irrigation may be a more sustainable way for drought mitigation, this may not be effective because rice irrigation is dependent on rainfall and in years of low rainfall, water supply is limited (Kimani, 2010). In addition, most small-scale farmers growing rice in the rainfed ecologies are resource constrained and cannot afford small and minor irrigation facilities. Therefore, cultivation of drought tolerant cultivars may perhaps be the best option for rice drought management in sub-Saharan Africa.

Approaches for development of drought resistant rice cultivars involve intensive screening of rice genotypes under drought conditions during either the vegetative, reproductive or ripening phase (Garrity and O'Toole, 1994; Fukai and Cooper, 1995). Of these growth stages, the reproductive stage is the most sensitive to water stress and grain yield of rice is reduced most when drought stress occurs during this stage (Rang *et al.*, 2011; He and Serraj, 2012). The strong effects of drought on grain yield are largely due to reduction of spikelet fertility and panicle exsertion (Wassmann *et al.*, 2009). Methods developed to screen rice genotypes for drought resistance at reproductive stage range from managed field stress environments (Garrity and O'Toole, 1994; Pantuwan *et al.*, 2002) to pot experiments (Lilley and Fukai, 1994; Wade *et al.*, 2000) under fully to semi-controlled conditions in greenhouses or in open fields. The former allows mass screening, while the latter is suitable for pre-breeding work such as evaluation of specific germplasm, parental lines or mapping population. Pot experiments used in this study eliminate the confounding effects of heterogeneity of soil and moisture supply commonly associated with field screening. They increase the precision with which pure genotypic differences can be detected. In situations where the test materials differ in maturity period, timing of stress in relation to the flowering date is of paramount importance (Garrity and O'Toole, 1994). Staggered planting is used to effectively synchronise flowering of test genotypes during the treatment period (Garrity and O'Toole, 1994).

To date, a number of morphological, physiological and integrative traits have been identified as indicators of drought resistance at reproductive growth stage in drought screening trials (Garrity and O'Toole, 1994; Garrity and O'Toole, 1995; Lilley and Fukai, 1994; Lafitte *et al.*, 2003). Among the integrative traits, spikelet fertility is the main yield component affected when stress occurs during the reproductive stage (Ekanayake *et al.*, 1989; Lafitte *et al.*, 2003). The genetic correlation between yield under stress and spikelet fertility is very high, and the heritability of spikelet fertility is less affected by stress than is the heritability of grain yield. So it gives clearer information on genotypic response to stress than does yield (Lafitte *et al.*, 2003). In addition to spikelet fertility, a few physiological traits have been recommended for application in drought breeding programmes (Lafitte *et al.*, 2003). Among them are relative water content, canopy temperature, leaf rolling and leaf drying scores (Lilley and Fukai, 1994; Garrity and O'Toole, 1995; Pantuwan *et al.*, 2002).

Several studies based on the above mentioned parameters have been conducted to identify drought tolerant rice genotypes (Lilley and Fukai, 1994; Garrity and O'Toole 1995; Lamo, 2009). Among four rainfed upland rice genotypes subjected to drought stress at reproductive stage, genotypic variability was observed for leaf rolling and leaf drying with the most sensitive cultivar (*Rikuto-Norin 12*) showing higher scores for leaf rolling and leaf death (Lilley and Fukai, 1994). In another study, Garrity and O'Toole (1995) reported that canopy temperature could aid in classification of genotypes for reproductive drought resistance because it was highly associated with grain yield, spikelet fertility, leaf rolling scores and visual drought tolerant scores. In Uganda, a study involving Asian, Africa and NERICA cultivars revealed significant variability for drought tolerance (Lamo, 2009). In this particular study (Lamo, 2009), when drought stress was imposed at reproductive stage, spikelet fertility varied from 26 to 92% among the genotypes. In addition, the study identified drought tolerance genotypes that included WAB 56-50, CT 16333(1)-CA-18-M, CT 16326-CA-3-M and NERICA 14 among others (Lamo, 2009).

Despite these studies, information on the drought tolerance of landraces, local and introduced cultivars in Kenya is unknown. Because the potential for expanding production of rainfed rice doubles that of irrigated, there is a great need for development of drought tolerant rice genotypes. Thus, identification of sources of drought tolerance from the traditional landraces, and genotypes from other breeding programmes would be useful for establishing drought tolerance breeding programme in rice. Therefore, the aim of this study was to determine genetic variability for drought tolerance at reproductive growth stage among the popular landraces, local cultivars, and exotic materials from the African-Rice Centre (ARC), the International Centre for Tropical Agriculture (CIAT) and the International Rice Research Institute (IRRI).

3.2 Materials and methods

3.2.1 Study location

The study was conducted on-station at Kenya Agricultural and Livestock Research Organisation (KALRO)-Mtwapa. KALRO-Mtwapa is located 20 km north of Mombasa in Kilifi South County, along Mombasa-Malindi road. It lies on latitude 3°50’S and longitude 39°44’E at an elevation of 15 m above sea level (masl). Annual mean temperatures are between 22°C and 26°C. The area receives bimodal mean rainfall of about 1200 mm with reliable long rains of 600 mm falling mid-March to July and the variable short rains of 250 mm falling in mid-October to December. The soils are dominated by orthic acrisols (80% sand) with low inherent fertility (Jaetzold and Schmidt, 1983). The typical agro-ecological zonation for KARLO-Mtwapa is coastal lowland three (CL3-coconut cassava zone).

3.2.2 Study lay out

The study was divided into two experiments, (1) Assessment of variability for drought tolerance in medium to late maturing genotypes under two conditions of no drought and drought, and (2) Assessment of variability for drought tolerance in early maturing genotypes under two conditions of no drought and drought.

3.2.3 Experiment 1: Medium to late maturing genotypes

3.2.3.1 Germplasm

The germplasm consisted of 15 rice genotypes. These cultivars had not been previously evaluated for tolerance to water stress under local environment. The source and characteristics of the genotypes are given in Table 3.1.

3.2.3.2 Treatments

The 15 medium to late maturing genotypes were evaluated in a steel and wire mesh screen house. Light, carbon dioxide concentration and temperature conditions were uncontrolled. The floor of the screen house was not cemented and instead it was covered with a white polythene paper to prevent roots imbibing water from the soil. The roof of the screen house was not covered and therefore plants could also receive rainfall. Genotypes were evaluated under no drought and drought stress conditions. The no drought stress evaluations were conducted in April to August 2013 (season I) and repeated in September 2013 to March 2014 (season II). In season 1, the experiment depended mostly on rainfall. However,

Table 3.1: Source, type and characteristics of the 15 medium to late maturing genotypes used in the study

Genotype	**Source***	**Species**	**Characteristics**
Kitumbo,	Kenya	*Oryza sativa*	Landrace, late, poor grain quality, moderate reproductive stage drought tolerance
Tuliani	Kenya	*Oryza sativa*	Local cultivar, late, good grain quality and highly aromatic
Supaa	Kenya	*Oryza sativa*	Local cultivar, late, good grain quality and highly aromatic
Kibawa Chekundu	Kenya	*Oryza sativa*	Landrace, late, low yielding, good for confectionery purposes
Shingo la Mjakazi	Kenya	*Oryza sativa*	Landrace medium to late, low yielding, good for confectionery purposes
Basmati 370	Kenya	*Oryza sativa*	Local cultivar, medium, drought susceptible, highly aromatic
Nerica L-19	ARC	Interspecific	Medium, long slender grains
Nerica L-25	ARC	Interspecific	Medium, long slender grains
Luyin 46	IRRI	*Oryza sativa*	Medium, high yielding, high tillering
IR10LL151	IRRI	*Oryza sativa*	Medium, high tillering
IR10LL176,	IRRI	*Oryza sativa*	Medium, high tillering
FKR19	ARC	*Oryza sativa*	Medium, good gain quality, high tillering
IR74371-54-1-1	IRRI	*Oryza sativa*	Medium, high reproductive stage drought tolerance, high yielding
IR55423-01	IRRI	*Oryza sativa*	Medium, moderate reproductive stage drought tolerance, high yielding,
AZUCENA	IRRI	*Oryza sativa*	Medium to late, reproductive stage drought susceptible

*IRRI, International Rice Research Institute; CIAT, International Center for Tropical Agriculture; ARC, Africa-Rice Centre (WARDA)

additional water was applied when necessary. In season II (Figure 3.1a) from transplanting to dough stage pots received one and half liters of water each during morning hours on daily basis and by the end of the day there was no standing water in each pot. Thereafter, watering was done after every two days to allow the plants to dry up for harvesting. The drought stress experiments were conducted in season II (Figure 3.1b). The number of days to flowering for each genotype was obtained from the non-water stress evaluations in season I. The genotypes were divided into two maturity groups in order to synchronise flowering. The late maturing group with days to flowering of more than 110 (Supaa, Tuliani, Kitumbo and Kibawa chekundu) was planted on 26 September 2013. The rest of the genotypes fell into the medium maturing group and were planted 35 days later. From transplanting to the time when drought was imposed, water application was the same as for the non-water stress. The number of days from planting to when the stress was imposed was 105 days for the late maturing and 70 days for the medium maturing. Drought stress was imposed at panicle initiation stage. At the beginning of the treatment, soil moisture in all pots was raised to 100% water holding capacity. The soil water content was monitored using watermark sensors installed in two pots per replication. Using a watermark meter model 200SS-5 designed to read watermark sensors exclusively, readings were monitored on daily basis and the average computed. Two consecutive drying cycles were imposed in order to prevent plants from dying and ensure they were stressed.

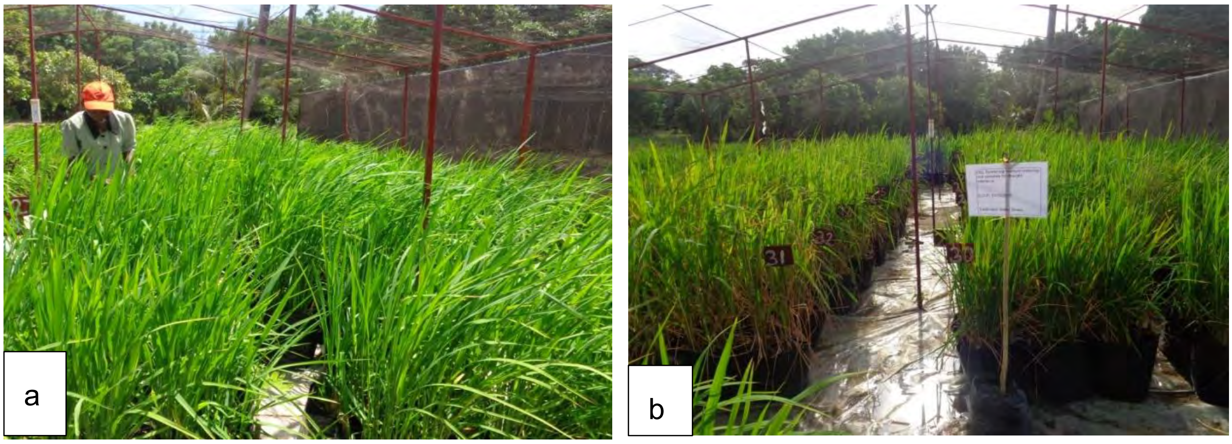

Figure 3.1: Screen house evaluations of the medium to late maturing genotypes; (a) no drought conditions and (b) drought conditions showing leaf senescence

3.2.4 Experiment 2: Early maturing genotypes

3.2.4.1 Germplasm

The germplasm consisted of six early maturing rice genotypes. These cultivars had not been previously evaluated for tolerance to water stress under local environment. The source and characteristics of the genotypes is given in Table 3.2.

Table 3.2: Source, type and characteristics of the 6 early maturing genotypes used in the study

Code	Genotype	Source*	Species	Characteristics
1	NERICA 1	ARC	Interspecific	Highly aromatic
2	NERICA 2	ARC	Interspecific	Slightly tolerant to drought
3	*Dourado precoce*	Kenya	*Oryza sativa*	Local cultivar, good grain quality, low yielding
4	CT16333(1) CA-22-M	CIAT	Interspecific	Good grain quality
5	CT16323-CA-25-M	CIAT	Interspecific	Low yielding, good grain quality
6	Vandana	IRRI	*Oryza sativa*	High reproductive stage drought tolerance, low yielding

*IRRI, International Rice Research Institute; CIAT, International Center for Tropical Agriculture; ARC, Africa-Rice Centre (WARDA)

3.2.4.2 Treatments

The materials were evaluated from December 2013 to March 2014. These were planted in black polyethylene pots set up in an open field. The ground where the experiment was set up was raised to about 15 cm above the ground level and the bare soil covered with a polythene paper to smoother weeds and to avoid root penetration into the soil. There were two treatments; no drought and drought treatment which were managed similar to treatments in experiment 1 (see section 3.2.3.2).

3.2.5 Experimental design and crop management in both experiments

In both experiments, the genotypes were planted in black polyethylene pots with 25 cm internal diameter and 30 cm height. Each pot was filled with 18 kg of sterilized soil mix of upland soil, sand and coconut coir dust in the ratio of 2:1:1 respectively. The experimental design for each treatment was randomized complete block design with four replications. The plot size was ten pots per entry. In each pot four seedlings were transplanted and spaced at 10 cm each to give a total of 40 plants per plot.

Seeds were first soaked in petri dishes for 24 hours to allow uniform germination. They were then transferred into seedling trays filled with sterile soil mix. On the twelfth day the seedlings were transplanted into polyethylene pots. Pots were watered to field capacity before planting. During planting, diamonium phosphate (DAP) was applied as a source of P. The P was applied at recommended rate of 60 kg P ha^{-1}. Source of N was calcium ammonium nitrate (CAN) which was top dressed at the rate of 120 kg N ha^{-1} applied in three splits of 40 kg ha^{-1} at 21 days after transplanting, tillering stage and at panicle initiation stage. Rice stem borer was effectively controlled using a synthetic pyrethroid. Weeds were controlled by hand picking. Harvesting was carried out manually.

3.2.6 Soil sampling in both experiments

From each experiment, 15 samples were collected from 15 planting pots from each treatment. The samples were bulked to form a composite and two sub-samples were taken per composite. The samples were submitted for analysis at NARL (National Agricultural Research Laboratories) soil analytical laboratories.

3.2.7 Data collection

Measurements of the drought related physiological characters namely, canopy temperature (CT), relative leaf water content (RLWC), leaf rolling (LR) and leaf drying (LD) were taken during the reproductive stage stress period which lasted for 14 days. The Standard Evaluation System (SES) for rice reference manual (IRRI, 1996) was used for all trait measurements except where stated. Measurements were taken as observed for the whole plot, otherwise, were stated. Canopy temperature was measured using infrared thermometer (IRT). Measurements we recorded from 11 to 13 h when there was little or no wind and the plant water deficit had been maximised. Two measurements were taken and the mean was computed. Relative leaf water content was determined between 12 and 14 h by the method suggested by Barrs and Weatherley (1962). From each plot 2-3 leaf samples constituting of mid leaf-section of about 5 – 10 cm were cut with scissors. Each sample was placed with its basal part to the bottom, in a pre-weighed airtight oven proof vial slightly longer than the samples. Vials were placed in a cooler box (10 to 15°C) and transported to the laboratory immediately. In the lab, vials were weighed to obtain leaf sample fresh weight (FW). After weighing de-ionized water was added to each vial and samples were left to hydrate for 24 hours under normal room light and temperature. After hydration samples were taken out of water, dried and immediately weighed to obtain fully turgid weight (TW). The samples were then oven dried at 80°C for 72 hours and weighed (after cooling in a dessicator) to determine the dry weight (DW). Relative leaf water content was calculated as: RLWC =

{(Fresh weight - Dry weight)/ (Turgid weight - Dry weight)} x 100. Leaf rolling was scored on a scale of 0 to 9: where 0, healthy leaves; 1, shallow V shaped leaves; 3, deep V-shaped leaves; 5, fully capped, u- shaped leaves; 7, leaf margins touching (0-shape); 9, tightly rolled leaves (IRRI 1996). During the period of drought imposition three scores were taken per plot and average was computed. Leaf drying was scored at the end of the stress period in the morning. A scale of 1 to 5 was used where 1 indicates no leaf death whereas 5 correspond to complete plant death. Three scores were taken per plot and average was computed.

Data on morphological, phenology, grain yield and it related traits, was collected on 10 competitive plants per plot. The plants were selected and tagged for data collection. Data collected were 50% flowering (DFL) determined visually when the central tiller of half of the selected had anthers exerted. Days to 50% heading (DH) determined visually when the central tiller of half of the selected had panicles exerted. Delay in flowering determined by subtracting days to 50% flowering under drought conditions from days to 50% flowering under no drought conditions. Plant height (PH) was measured at maturity stage using a calibrated meter scale from soil surface to tip of the tallest panicle (awns excluded). Number of tillers per plant (TLA) was recorded by counting the number of productive tillers per hill. Panicle length (PNL) was measured at maturity stage using a calibrated meter scale from panicle base to tip. Number of grains per panicle (NGPP) was obtained from the difference between the total number of spikelets and unfilled spikelets. One thousand seeds weight (TGW) was obtained by individually counting 100 well developed whole grains. Twenty samples were counted, dried to a moisture content of 14% and weighed using an electronic balance. The final weight was then converted to 1000 grain weight by multiplying by 10. Spikelet fertility was determined as described by Lafitte *et al.* (2003). Twenty panicles were randomly selected from each plot. Spikelet fertility was scored as; highly fertile (>90%); fertile (75-89%); partly sterile (50-74%); highly sterile (<50% to trace) and completely sterile (0%). Grain yield per plant was determined from ten selected plants from each plot. The grain was harvested manually, hand threshed, and the grains dried to achieve a moisture content of 14%. The moisture content was determined using a moisture meter. The grain was weighed in grams using digital electronic balance. The mean grain weight obtained from the ten plants was computed to give grain yield per plant in grams.

Drought tolerance index: The effects of drought on each genotype were determined by calculating the drought tolerance index = [(X control – X stress)/X control)] * 100, where X is the trait value.

3.2.8 Data analysis

The analysis of variance (ANOVA) to determine differences between genotypes was computed separately on individual experiments for all characters. This was performed according to (Gomez and Gomez, 1984) using GenStat statistical package version 14 (Payne *et al.*, 2011). The treatment and genotype means were separated using the least significant differences (LSD) test. Simple linear correlation analysis was also computed.

To determine drought tolerance of the genotypes, a selection index as suggested by (Bänziger et al., 2000) was used to summarise the worth of each genotype. Weights (Wi) were assigned based on the relative value of each trait as an indicator of drought stress in upland rice ecology. The phenotypic values, Pi, were standardized, as: $Pi = (xij - mi)/sdi$; where mi and sdi are the mean and standard deviation of trait i in the experiment, and xij is the value of the trait i measured on genotype j. A selection index I for each genotype was then computed as: $I = W1P1 + W2P2 + \dots. WnPn$ where Pi is the observed standardized value of the trait i and Wi is the weight assigned to that trait in the selection index. The weight were determined based the correlation of the trait with grain yield and ease of measurement and repeatability of each trait in the field. The checks were used for rating drought tolerance and susceptibility of the other genotypes.

3.3 Results

3.3.1 Weather condition

During the period of study the highest amount of rainfall of 391 mm occurred during May 2013 (Figure 3.2). There was no rainfall received in January 2014 while in February 2014 13 mm of rainfall were received towards the end of the month. Drought screening was imposed in January 2014 for medium to late maturing genotypes and beginning of February 2014 for early maturing genotypes. The daily maximum temperature ranged between 27-34^{o}C (mean 30^{o}C), while the minimum temperature ranged between 18-27^{o}C (mean 23^{o}C). Relative humidity ranged between 65-96% (mean 77%). Daily wind speed ranged from 7 to 389 miles per day (mean of 100 miles per day).

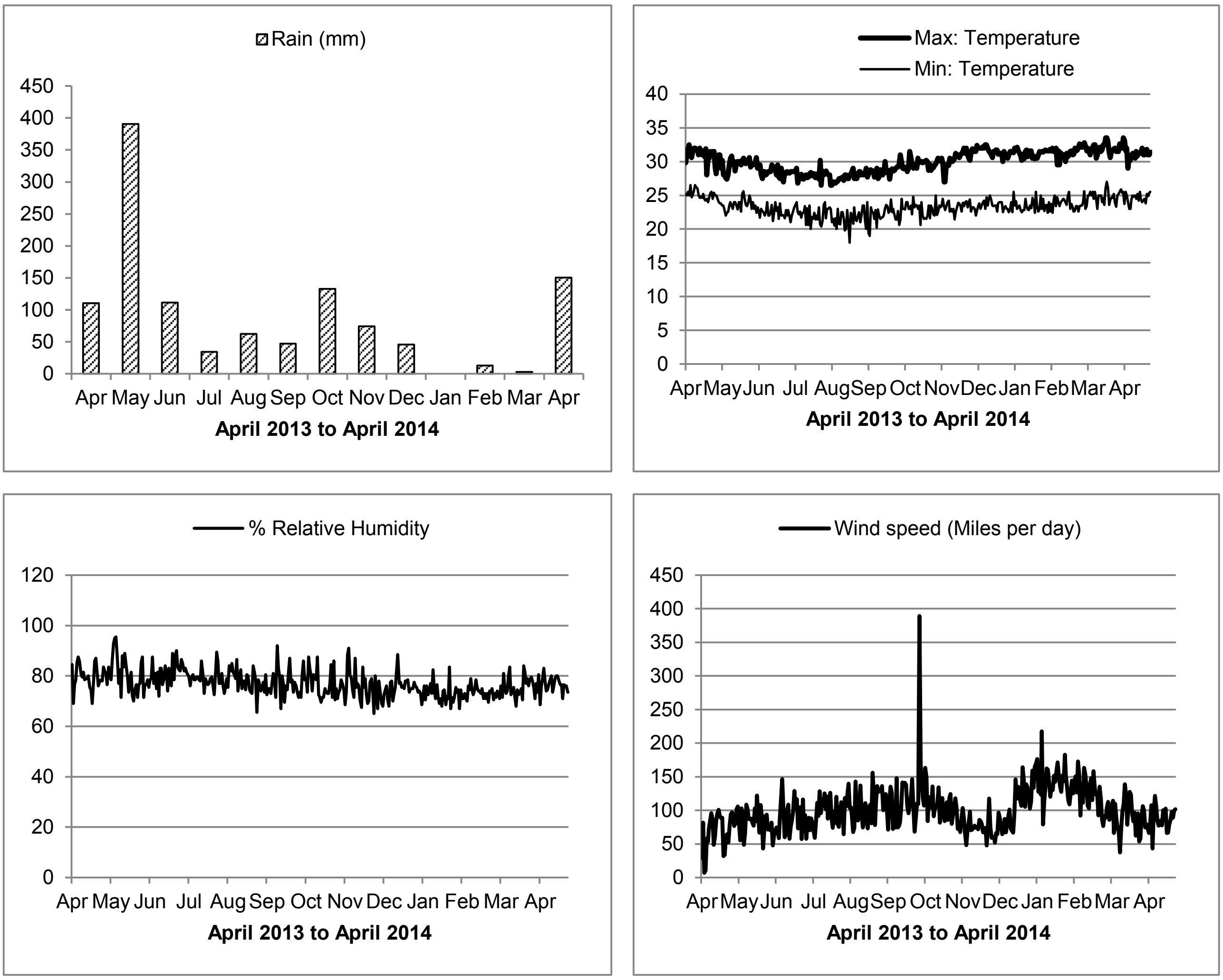

Figure 3.2: A graph showing from left to clockwise direction; rainfall in mm, maximum and minimum temperature (^{0}C), wind speed in miles per day and relative humidity (%) during the period of study

3.3.2 Soil chemical properties for Experiment I and II

The soils were classified as slightly acidic with low %N and organic carbon (Table 3.3). The soil texture was sandy loam with very low cation exchange capacity of 12 (meq/100g) predisposed by the low percentage of clay and organic matter. The rest of the minerals were adequate to high.

Table 3.3: Chemical analysis of the macro and micro nutrients of the sterilized planting soil media used in season I and II.

Parameter	Value	Class
Soil pH	6.50	Slightly acidic
Total Nitrogen %	0.15	Low
Total organic carbon %	1.42	Low
Phosphorus ppm‡	45.00	High
Potassium ppm	397.80	adequate
Calcium ppm	540.00	adequate
Magnesium ppm	811.91	High
CEC†	12.00	Low
Sand%	86.00	High
Silt%	8.00	Low
Clay%	6.00	Low
Soil texture	Loam sandy	

‡ppm, parts per million; † CEC, cation exchange capacity

3.3.3 Experiment 1: Medium to late maturing genotypes

3.3.3.1 Monitoring the drought stress condition

Two consecutive drying cycles of drought stress were imposed (Figure 3.3). In the first cycle, soil moisture tension increased from 0 to 79 centibars by the eighth day. Most plants had started showing symptoms of wilting. On the 9th and 10th day of water stress, soil moisture in all pots was raised to 100% water holding capacity. The second cycle of water stress was imposed on the 11th day. During the second cycle, soil moisture tension increased from 0 to 81 centibars by the seventh day. Thereafter, the soil moisture tension was maintained at between 30 to 40 centibars until harvesting. Fast soil dehydration was observed when irrigation was stopped. This was attributed to the characteristics of the potting media which were 86% sandy and low in organic matter.

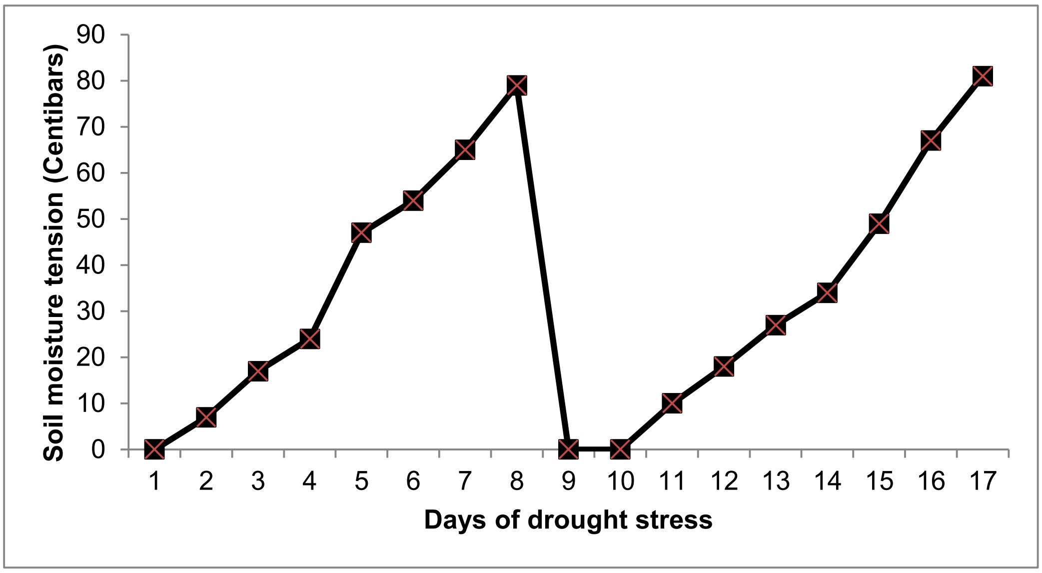

Figure 3.3 Soil moisture tension in centibars during the two cycles of drought screening medium to late maturing genotypes

3.3.3.2 Performance of genotypes under no drought conditions in season 1

The results showed that genotypes exhibited highly significant differences (P<0.001) for all the traits measured under no drought conditions in season 1 (Table 3.4). The average grain yield per plant was 26 g ranging from 17 to 36 g (Table 3.5). The highest yielding genotype was Luyin 46 (36 g). Among the local cultivars Tuliani (25 g) was the best performer followed by Basmati 370 (23 g). Mean days to flowering was 88 days and ranged from 67 days for CT16333(1)-CA-22 to 114 days for Supaa and Tuliani. The shortest genotype was IR10L176 (99 cm) while Supaa, Tuliani, Shingo la Mjakazi, Kibawa Chekundu and Azucena were tall showing a plant height of over 150 cm. Tillering ability was highest (12 tillers) for IR10L151 and IR10L176 and lowest (7) for genotypes Supaa, Tuliani, Azucena and CT16333(1)-CA-22. The average number of grains per panicle was 161 grains. Tuliani had the highest number of grains per panicle (207) while CT16333(1)-CA-22 showed the lowest number of 100 grains.

The results for season I were made to capture the phenology and morphological characteristics of the 15 genotypes used in experiment 1. Days to flowering for these genotypes under humid conditions of coastal Kenya was not known. The results were therefore used to group the genotypes into late and medium maturing and to stagger planting in season II to allow synchronization of the reproductive stage of all the genotype for the drought stress treatment.

Table 3.4: Mean squares for phenology, plant height, tiller number, grain yield per plant and its contributing traits among 15 rice genotypes evaluated under no drought conditions in April to August 2013 at KALRO Mtwapa Kenya

		Mean squares							
Source of variation		DH†	DFL	PH	TLA	PNL	NGPP	TGWT	GYP
	df	Days	Days	cm	#	cm	#	g	G
BLOCK	3	2.59	3.33	18.73	5.44	1.03	59.40	8.09	109.63
GENOTYPE	14	671.5**	814.8**	2002.2**	15.4**	26.3**	4555.3**	51.9**	114.8**
RESIDUAL	42	1.19	1.62	35.65	1.99	1.75	422.90	2.25	15.83

*, **, ***, Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant

† DH, Days to 50% heading; DFL, Days to 50% flowering; PH, Plant height; TLA, Tiller number; PNL, Panicle length; NGPP, Number of grains per panicle; TGWT, One thousand grain weight; GYP^{-1}, Grain yield per plant.

Table 3.5: Mean values for phenology, plant height, tiller number, grain yield per plant and its contributing traits among 15 rice genotypes evaluated under no drought conditions in April to August 2013 at KALRO Mtwapa Kenya

Genotypes	Mean values							
	DH	DA	PH	TLA	PNL	NGPP	TGWT	GYPP
	Days	Days	cm	#	cm	#	g	G
Bas 370	79	80	139	13	24	112	22.49	23.87
CT16333(1)-CA-22	65	68	122	7	28	100	31.48	23.96
NERICA-L-19	87	90	137	9	25	165	26.15	25.00
LUYIN 46	78	80	119	10	21	204	25.34	36.39
IR10L151	79	80	102	12	21	144	27.75	33.82
IR10L176	84	85	99	12	22	129	24.94	27.35
NERICA-L-25	79	80	132	10	28	200	23.81	27.60
AZUCENA	87	90	157	7	28	163	31.46	22.84
IR74371-54-1-1	76	78	113	10	23	168	23.91	31.61
FKR19	76	78	104	11	23	172	26.35	28.27
IR55423-01	86	87	112	10	23	180	24.24	31.13
Tuliani	109	114	156	7	28	207	33.53	25.46
Kibawa Chekundu	107	112	148	10	24	143	24.30	17.36
Shingo la Mjakazi	85	89	168	8	26	129	30.98	20.73
Supaa	109	114	153	7	28	197	31.48	19.33
MEAN	**86**	**88**	**131**	**10**	**25**	**161**	**27**	**26**
LSD(0.05)	**1.56**	**1.82**	**8.52**	**2.01**	**1.86**	**29.34**	**2.14**	**5.68**
%CV	**0.50**	**0.50**	**0.90**	**6.30**	**1.1**	**1.20**	**2.70**	**10.30**

CV; Coefficient of variation

† DH, Days to 50% heading; DFL, Days to 50% flowering; PH, Plant height; TLA, Tiller number; PNL, Panicle length; NGPP, Number of grains per panicle; TGWT, One thousand grain weight; GYP^{-1}, Grain yield per plant

3.3.3.3 Performance of genotypes under drought and no drought in season II

Mean squares due to genotypes under no drought conditions were highly significant at $p<0.001$ for days to 50% flowering, spikelet fertility and grain yield per plant and non-significant for all the physiological traits (Table 3.6). Under drought conditions highly significant ($p<0.001$) differences among genotypes were observed for all the traits measured. Across environments mean squares due to environment (E) and genotype (G) main effects were highly significant at $p<0.001$ for all the traits measured. The GxE interactions were significant ($p<0.05$) for canopy temperature and highly significant ($p<0.001$) for all the other traits. Under no drought conditions statistical differences among genotypes were pronounced for grain yield per plant, spikelet fertility and days to 50% flowering, marginal for canopy temperature and relative leaf water content and no differences observed for leaf rolling and leaf drying (Table 3.7). Under drought conditions marked statistical differences were observed for all the traits measured.

Table 3.6: Mean squares for physiological traits, grain yield per plant, spikelet fertility and days to 50% flowering among 15 rice genotypes evaluated under drought and no drought conditions at KALRO Mtwapa Kenya

Source of variation	df	Mean squares						
		CT† °C	RLWC %	LR Score	LD Score	DFL Days	SF %	GYP^{-1} g
No drought conditions								
BLOCK	3	7.72	0.31	0	0	19.31	75.87	291.15
GENOTYPE	14	2.57^{ns}	6.52^{ns}	0	0	987.59***	3155.03***	2994.85***
RESIDUAL	42	2.21	4.74	0	0	7.12	964.42	827.52
CV		2	0.2	0	0	1.2	1.5	10.1
Drought conditions								
BLOCK	3	3.11	101.64	0.31	0.33	8.15	118.42	20.17
GENOTYPE	14	13.76***	308.73***	10.80***	1.99***	1188.16***	346.24***	129.11***
RESIDUAL	42	3.45	51.25	1.42	0.16	9.77	53.94	26.76
CV		1.6	4.5	2.3	4.4	2.7	5.3	10.7
Across								
ENV	1	621.08**	26669.82**	832.13**	165.68**	1548.01**	31145.03**	6235.33**
REP(ENV)	3	5.55	48.98	0.16	0.16	27.74	130.25	72.47
GENOTYPE	14	9.88**	150.56**	5.40**	1.00**	2316.39**	332.60**	286.95**
ENV*GENOTYPE	14	6.45*	164.67**	5.40**	1.00**	20.58**	198.23**	56.07**
RESIDUAL	84	2.83	28	0.71	0.08	7.28	39.07	23.23
CV		6.34	7.31	23.18	13.05	2.74	8.91	26.74

*, **, ***, Significant at $p < 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant

CV, Coefficient of variation;

† CT, Canopy temperature; DFL, Days to 50% flowering; GYP^{-1}, Grain yield per plant; RLWC, Relative Leaf Water Content; LR, Leaf rolling; LD, Leaf drying; SF, Spikelet fertility.

Table 3.7: Mean values of 15 medium to late maturing genotypes evaluated under drought and no drought conditions in a screen house at KALRO-Mtwapa, Kenya

Genotype	Mean values													
	CT†		RLWC		LR		LD		DFL		SF		GYP^{-1}	
	DRT*	NO DRT	DRT	NO DRT	DRT	NO DRT	DRT	NO DRT	DRT	NO DRT	DRT	NO DRT	DRT	NO DRT
Kitumbo	27	26	53.38	87.50	5.50	1.00	4	1.00	126	121	54.38	73.93	8.95	17.29
Tuliani	31	25	52.98	89.50	7.50	1.00	4	1.00	131	118	52.03	74.12	6.88	21.62
Supa	30	25	56.75	89.25	7.00	1.00	4	1.00	132	121	51.79	73.53	7.06	16.39
Kibawa Chekundu	32	25	54.14	88.50	8.50	1.00	4	1.00	127	117	50.89	82.38	5.03	13.32
Shingo la Mjakazi	27	25	69.60	85.50	4.00	1.00	2	1.00	97.5	95	54.86	91.60	10.30	19.53
Bas 370	30	25	44.67	85.75	8.00	1.00	4	1.00	96	84	38.49	85.57	6.55	21.81
Nerica L-19	27	24	54.73	87.50	7.00	1.00	3	1.00	97	89	60.16	89.19	15.94	29.72
Nerica L-25	32	24	39.10	87.75	7.25	1.00	4	1.00	99	85	41.56	81.60	5.29	25.02
Luyin 46	28	24	56.26	87.00	6.00	1.00	4	1.00	91	85	63.82	89.02	19.94	31.65
IR10LL151	29	24	65.02	86.75	6.00	1.00	4	1.00	90	83	40.57	89.01	7.79	30.08
IR10LL176	28	24	60.43	87.50	6.00	1.00	3	1.00	96	89	60.11	90.19	18.28	37.04
FKR19	28	23	53.67	85.50	7.00	1.00	3	1.00	94	80	44.78	95.42	6.56	30.98
IR74371-54-1-1	26	23	68.49	86.00	2.50	1.00	2	1.00	78	78	70.39	95.59	21.04	30.55
IR55423-01	27	24	66.67	88.50	4.25	1.00	2	1.00	90	88	63.83	91.75	15.76	34.45
AZUCENA	29	24	66.87	87.50	7.50	1.00	4	1.00	102	94	52.80	90.88	6.93	19.08
Mean	**29**	**24**	**57.52**	**87.33**	**6.27**	**1.00**	**3.32**	**1.00**	**103**	**95**	**53.36**	**86.25**	**10.82**	**25.24**
LSD (0.05)	**2.65**	**2.12**	**10.22**	**3.11**	**1.70**	**0.00**	**0.57**	**0.00**	**4.46**	**4**	**10.48**	**6.84**	**7.38**	**6.33**

† CT, Canopy temperature; RLWC, Relative Leaf Water Content; LR, Leaf rolling; LD, Leaf drying; DFL, Days to 50% flowering; SF, Spikelet fertility; GYP^{-1}, Grain yield per plant

*DRT, Drought; NO DRT, No Drought

3.3.3.4 Effects of drought on physiological traits

The response of genotypes to drought stress varied among genotypes. Drought stress increased canopy temperature of all the genotypes with an average increase of 5°C between the mean canopy temperature in the drought and no drought conditions. Canopy temperature was coolest for IR74371-54-1-1 (26°C) and warmest (32°C) for NERICA-L-25 and Kibawa chekundu (Table 3.7). Kitumbo showed the lowest relative increase of 6% while NERICA-L-25 had the highest relative increase of 36% (Figure 3.4). The average relative leaf water content under drought conditions was 58% compared to 87% under no drought conditions. Shingo la Mjakazi showed the highest relative leaf water content of 70% followed by IR74371-54-1-1 (68%), IR55423-01 (67%), AZUCENA (67%) and IR10LL151 (65%) in that rank order. Genotype NERICA-L-25 had the lowest relative leaf water content of 39% followed by Basmati 370 (45%). Relative decrease in relative leaf water content ranged from 19 to 55% with a mean of 34% (Figure 3.5). Genotypes IR10LL151, IR74371-54-1-1, AZUCENA, IR55423-01 and Shigo la Mjakazi showed the lowest decrease of 25% and below. Drought stress reduced relative leaf water content of NERICA-L-25 by 55%. Leaf rolling of all the genotypes was affected by drought stress ranging from deep V shaped (score of 3) to tightly rolled leaves (score of 9) (Figure 3.6). All the genotypes showed signs of leaf drying from slight (score of 2) to severe (score of 4) (Figure 3.7). The tolerant check showed the lowest leaf rolling and leaf drying scores of 3 and 2 respectively followed by the moderately drought tolerant check and Shingo la Mjakazi. Kibawa chekundu performed poorly with leaf rolling and drying scores of 9 and 4, respectively.

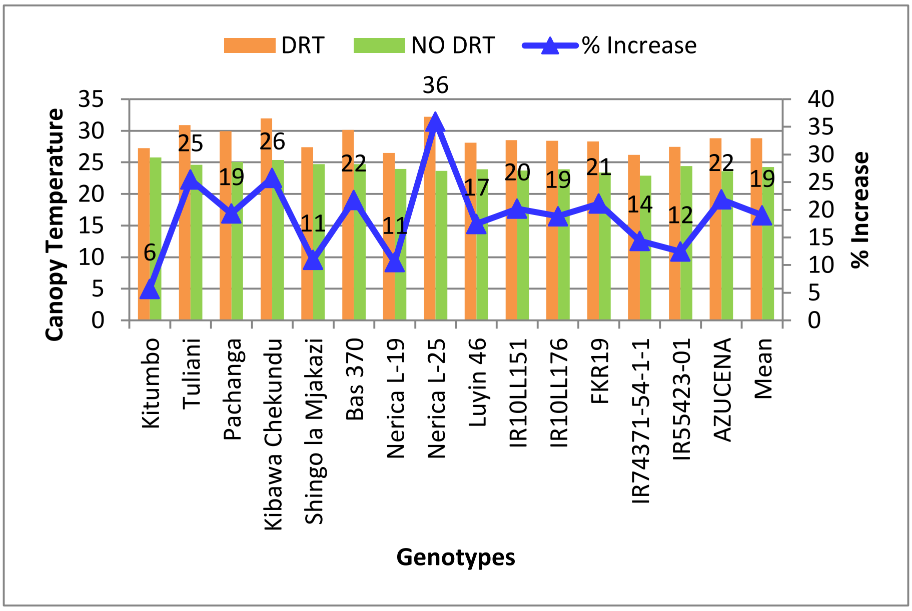

Figure 3.4: Relative canopy temperature increase under drought (DRT) compared to no drought (NO DRT) conditions

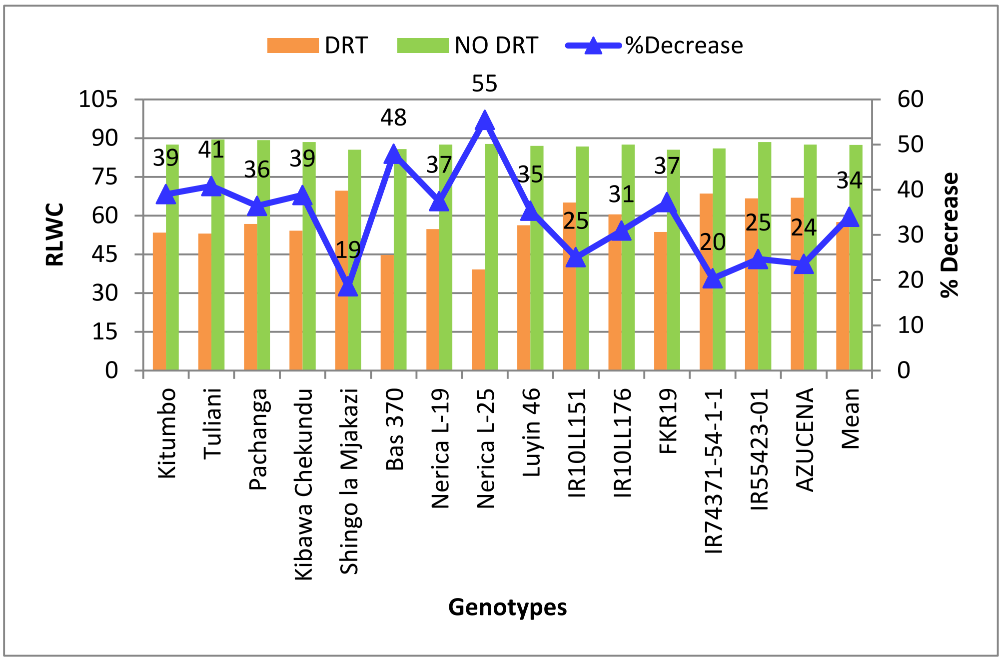

Figure 3.5: Relative relative leaf water content (RLWC) decrease under drought (DRT) compared to no drought (NO DRT) conditions

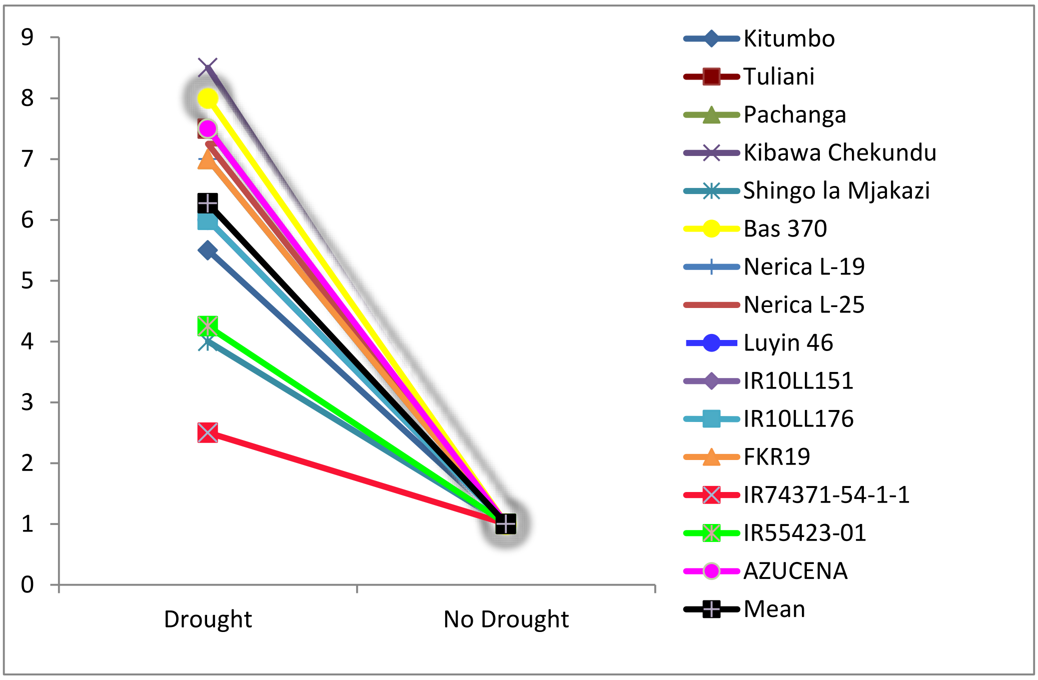

Figure 3.6: Changes in leaf rolling of rice genotypes under drought and no drought conditions

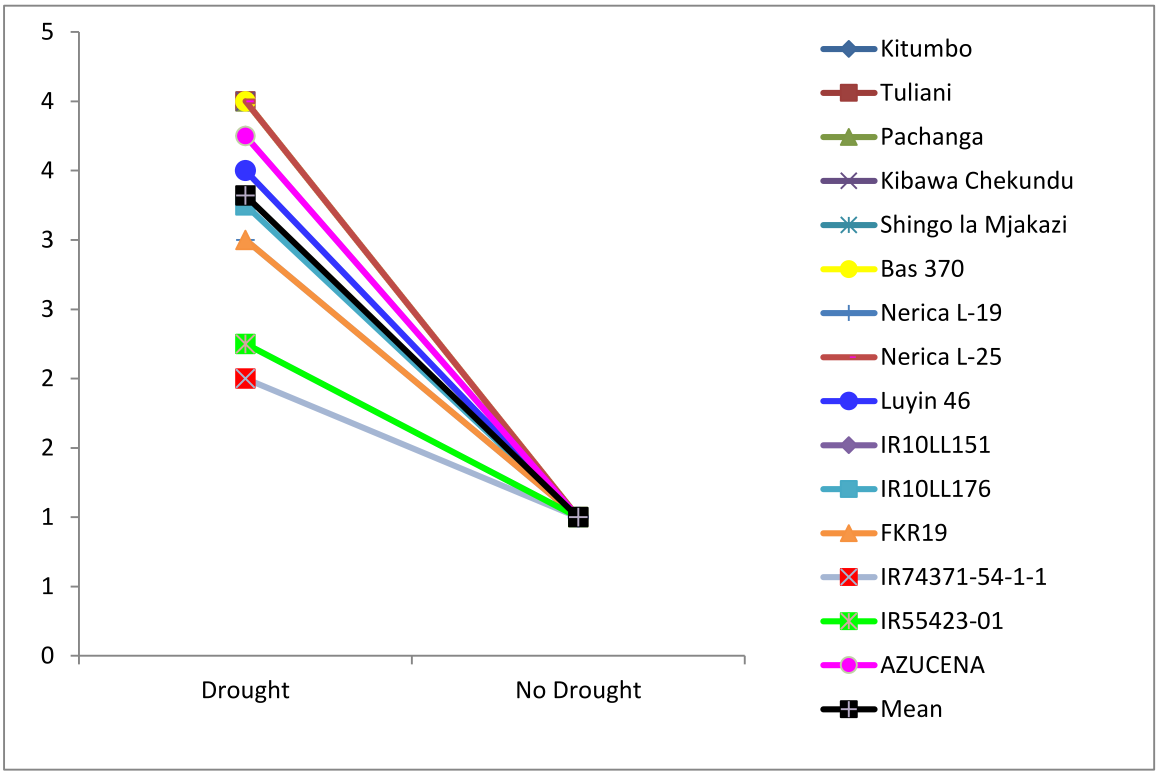

Figure 3.7: Changes in leaf drying of rice genotypes under drought and no drought conditions

3.3.3.5 Effects of drought stress on grain yield plant^{-1}, spikelet fertility and days to 50% flowering,

Grain yield per plant under drought conditions ranged from 5 to 21 g plant^{-1} with an average of 11 g plant^{-1} compared to 25 g plant^{-1} under no drought conditions. Grain yield of sixty six percent of the genotypes mostly the local cultivars was below 10 g plant^{-1}. The overall mean relative grain yield reduction was 57% (Figure 3.8). Genotype IR74371-54-1 showed the least grain yield reduction of 31% followed by Luyin 46, NERICA-L-19, Shingo la mjakazi and Kitumbo in that rank order. Genotype FKR19 and NERICA-L-25 showed the highest relative yield reduction of 79%. Relative yield reduction of the rest of the genotypes ranged from 51 to 74%. Relative spikelet fertility ranged from 26 to 55% with a mean of 37% (Figure 3.9). Spikelet fertility of 80% of the genotypes was partly sterile (50-74%) with the rest showing high spikelet sterility (<50% to trace). Kitumbo and IR74371-54-1 showed the lowest relative spikelet fertility reduction of 26%. Genotype Basmati 370 and IR10LL151 had the highest relative spikelet fertility reduction of 55 and 54% respectively. Delay in flowering ranged from 0 to 14 days with a mean of 8 days (Figure 3.10).

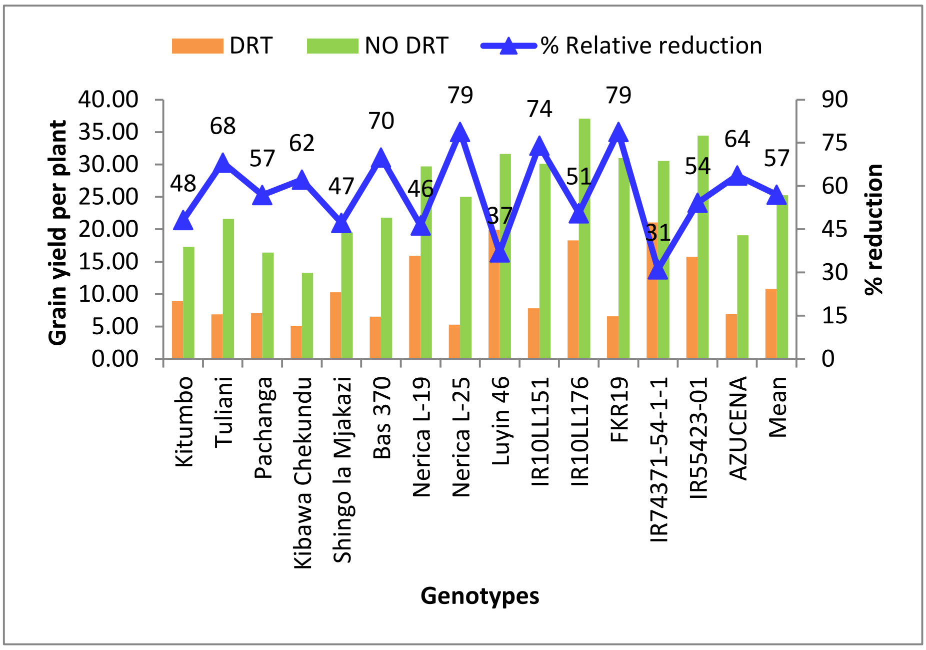

Figure 3.8: Relative yield reduction of rice genotypes under drought (DRT) compared to no drought (NO DRT) conditions

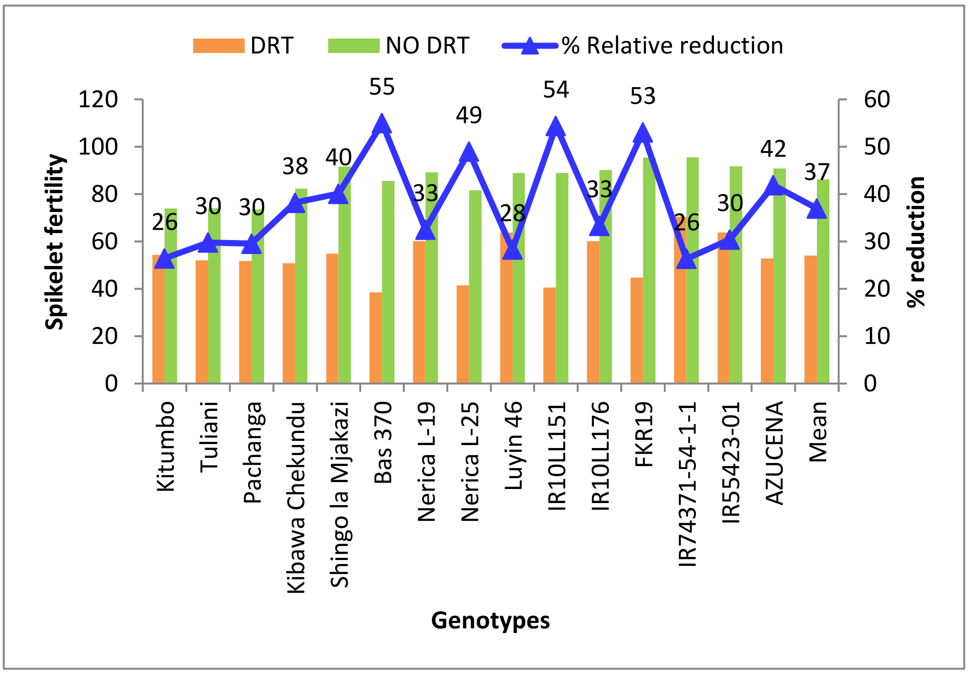

Figure 3.9: Relative spikelet fertility reduction of rice genotypes under drought (DRT) and no drought (NO DRT) conditions

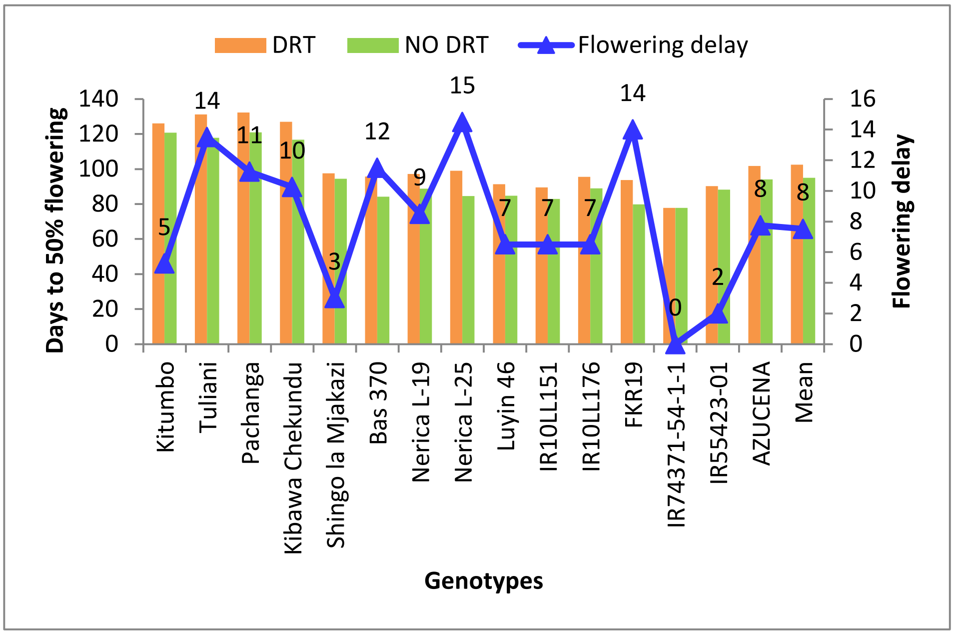

Figure 3.10: Flowering delay of rice genotypes under drought (DRT) and no drought (NO DRT) conditions

3.3.3.6 Selection index

Weighted indices and a selection index were used to select drought tolerant and susceptible genotypes (Table 3.8). The selection index was based on canopy temperature, leaf rolling, relative leaf water content, grain yield per plant and spikelet fertility. Leaf rolling was correlated with leaf drying and therefore the latter was eliminated from the selection index. Days to 50% flowering was not included in the selection index due to a large variation among genotypes. Weights assigned for each trait were; canopy temperature 3, relative leaf water content 1, leaf rolling 3, spikelet fertility 4 and grain yield per plant 5.

Genotypes with negative values for canopy temperature and leaf rolling were more desirable. IR74371-54-1-1 had the lowest negative values for canopy temperature (-3.27) and leaf rolling (-5.97) (Table 3.8). Other genotypes with low values for canopy temperature were NERICA-L-19 (-2.86), Kitumbo (-1.91) and Shingo la Mjakazi (-1.75) in that rank order. For leaf rolling a traditional cultivar Shingo la Mjakazi, was the second best after IR74371-54-1-1 with a value of -3.60 followed by IR55423-01 (-3.20). Genotypes with positive values for relative leaf water content were more desirable. Shingo la Mjakazi had the highest value of 1.13 followed by IR74371-54-1-1. For grain yield per plant and spikelet fertility all values were positive and larger values were more desirable. Once more IR74371-54-1-1 had the highest values for these traits followed by Luyin 46.

Table 3.8: Selection based on selection index of physiological traits, grain yield per plant and spikelet fertility under drought conditions

Genotype	CT†	RLWC	LR	SF	GYP^{-1}	SI
Kitumbo	-1.91	-0.39	-1.22	0.37	0.58	-2.56
Tuliani	2.59	-0.42	1.95	0.35	0.45	4.91
Supa	1.41	-0.07	1.16	0.35	0.46	3.31
Kibawa Chekundu	3.89	-0.32	3.53	0.34	0.33	7.78
Shingo la Mjakazi	-1.75	1.13	-3.60	0.37	0.67	-3.18
Bas370	1.62	-1.20	2.74	0.26	0.43	3.85
Nerica L-19	-2.86	-0.26	1.16	0.41	1.03	-0.52
Nerica L-25	4.20	-1.72	1.55	0.28	0.34	4.66
Luyin 46	-0.88	-0.12	-0.43	0.43	1.29	0.30
IR10LL151	-0.36	0.70	-0.43	0.27	0.51	0.69
IR10LL176	-0.51	0.27	-0.43	0.41	1.19	0.93
FKR19	-0.61	-0.36	1.16	0.30	0.43	0.92
IR74371-54-1-1	-3.27	1.02	-5.97	0.48	1.37	-6.38
IR55423-01	-1.66	0.85	-3.20	0.43	1.02	-2.55
Azucena	-0.01	0.87	1.95	0.36	0.45	3.62

† CT, Canopy temperature; RLWC, Relative Leaf Water Content; LR, Leaf rolling; SF, Spikelet fertility; GYP^{-1}, Grain yield per plant; SI, Selection index

Overall the selection index (SI) values ranged from -6.38 to 7.78. The checks were used for classification of genotypes based on selection index value (Table 3.9). The highly drought tolerant check (IR74371-54-1-1) was exceptional with a SI of -6.38 and therefore rated highly tolerant. Shingo la Mjakazi and Kitumbo fell in the same class with the moderately tolerant check and were rated moderately tolerant. Genotypes NERICA-L-25, Tuliani and Kibawa Chekundu were found to be highly susceptible.

Table 3.9: Classification of levels of drought tolerance of the 15 rice genotypes based on selection index values and checks as the reference genotypes

Class	Rating	Genotypes
≤ -6	Highly tolerant	IR74371-54-1-1
-5.9 to -4	Tolerant	None
-3.9 to -2	Moderately tolerant	Kitumbo, Shingo la Mjakazi and IR55423-01
-1.9 to 1.9	Moderately susceptible	Nerica L-19, Luyin 46, IR10LL151, IR10LL176, and FKR19
2 to 3.9	Susceptible	Azucena, Bas370 and Pachanga
≥4	Highly susceptible	Nerica L-25, Tuliani and Kibawa chekundu

3.3.3.7 Association of characters

Association of characters was investigated under both drought and no drought conditions, but only the results on association of characters under drought conditions are presented in Table 3.10. Under no drought conditions only significant and positive association was observed between grain yield per plant and spikelet fertility (0.55***) and negative association between grain yield per plant and days to 50% flowering (-0.59***). The rest of the traits did not show any significant association with grain yield per plant. Under drought conditions association between grain yield per plant and the other traits were significant and negative for canopy temperature, leaf rolling and leaf drying and days to 50% flowering, and significant and positive for relative leaf water content and spikelet fertility. Drought related parameter canopy temperature was significantly and positively correlated with leaf rolling and leaf drying. Relative leaf water content showed a significant and negative correlation with all the other physiological traits. Spikelet fertility was found to be significantly and negatively correlated with relative leaf water content and negatively with canopy temperature, leaf rolling and leaf drying.

Table 3.10: Phenotypic correlation coefficients between grain yield plant^{-1} and physiological traits, days to 50% flowering and spikelet fertility under drought conditions

Plant characteristics	**GYP^{-1}**	**CT**	**RLWC**	**LR**	**LD**	**DFL**
Grain yield per plant(GYP^{-1})						
Canopy temperature (CT)	-0.43**					
Relative leaf water content (RLWC)	0.35**	-0.35**				
Leaf rolling (LR)	-0.50***	0.58***	-0.38**			
Leaf drying (LD)	-0.48***	0.55***	-0.43**	0.68***		
Days to 50% flowering (DFL)	-0.39**	0.37**	-0.18ns	0.45***	0.43**	
Percent spikelet fertility (SF)	0.62***	-0.42**	0.30*	-0.40**	-0.44***	-0.31*

*, **, ***, Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant

3.3.4 Experiment 2: Early maturing genotypes

3.3.4.1 Monitoring the drought stress condition

Two consecutive drying cycles of drought stress were imposed (Figure 3.11). In the first cycle, soil moisture tension increased from 0 to 89 centibars by the eighth day. Most plants had started showing symptoms of wilting. On the 9th and 10th day of water stress, soil moisture in all pots was raised to 100% water holding capacity. The second cycle of water stress was imposed on the 11th day. During the second cycle, soil moisture tension increased from 0 to 87 centibars by the eighth day. Thereafter the soil moisture tension was maintained at between 30 to 40 centibars until harvesting.

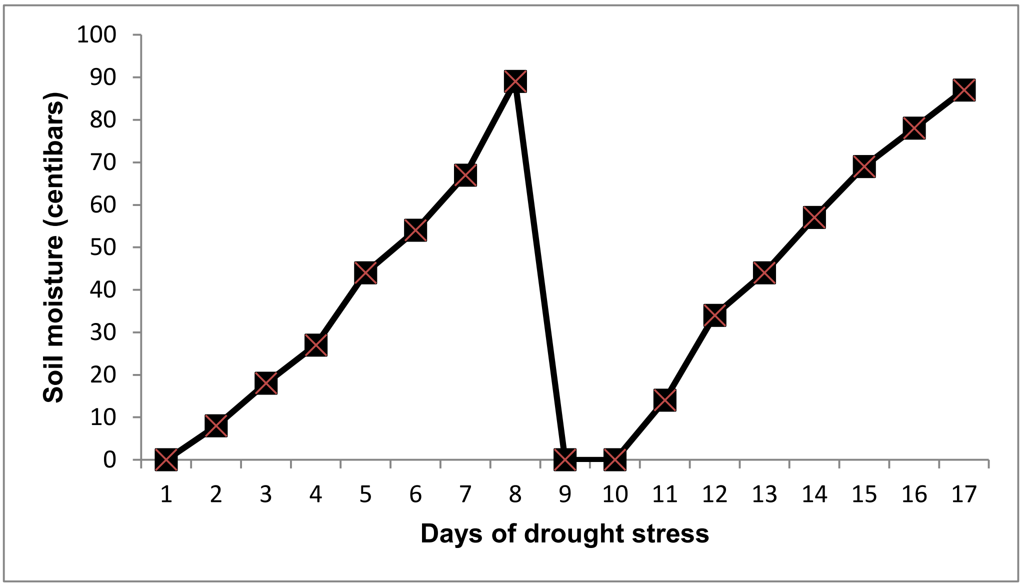

Figure 3.11: Soil moisture content in centibars during the two cycles of drought screening early maturing genotypes

3.3.4.2 Performance of genotypes under drought and no drought conditions

Mean squares due to genotypes were highly significant at P≤0.001 for days to 50% flowering and non-significant for leaf rolling, relative leaf water content and spikelet fertility under no drought conditions (Table 3.11). Under drought conditions highly significant (P≤0.001) differences among genotypes were observed for leaf rolling, days to 50% flowering and spikelet fertility and non-significant differences for relative leaf water content. Across environments mean squares due to environment (E) main effects were highly significant at P≤0.001 for all the traits measured. The differences among genotypes and their interaction with the environment were non-significant for relative leaf water content and significant at P≤0.05 for leaf rolling, days to 50% flowering and spikelet fertility. Under no drought conditions there were no statistical differences among genotypes for leaf rolling whereas marginal statistical differences were observed for the rest of the traits (Table 3.12). Under drought conditions marginal statistical differences were observed among genotypes for relative leaf water content and pronounced differences observed for the rest of the traits measured.

Table 3.11: Mean squares for leaf rolling, relative leaf water content, days to 50% flowering and spikelet fertility of six early maturing genotypes

Source of variation	**df**	**Mean squares**			
		LR† Score	RLWC %	DFL Days	SF %
		No drought			
BLOCK	3	0.00	7.38	7.00	15.08
GENOTYPE	5	0.00	6.18^{ns}	61.67***	20.29^{ns}
RESIDUAL	15	0.00	6.58	5.33	13.27
CV		0.00	1.30	1.70	1.70
		Drought			
BLOCK	3	0.67	31.86	17.00	182.87
GENOTYPE	5	19.47***	65.11^{ns}	124.97***	713.27***
RESIDUAL	15	1.42	34.72	5.70	98.11
CV		5.00	1.90	1.40	5.30
		Across environments			
ENV	1	96.33***	4320.34***	261.33***	11478.81***
REP(ENV)	3	0.11	4.30	6.06	59.07
GENOTYPE	5	9.73***	21.10^{ns}	169.95***	316.41***
ENV*GENOTYPE	5	9.73***	50.19^{ns}	16.68*	417.15***
RESIDUAL	30	0.71	20.65	5.52	55.69
CV		34.89	5.83	3.48	9.80

*, **, ***, Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively; ns, non-significant

CV; Coefficient of variation

†DFL, Days to 50% flowering; GYP^{-1}, Grain yield per plant; RLWC, Relative Leaf Water Content; LR, Leaf rolling; SF, Spikelet fertility; CV, Coefficient of Variation

3.3.4.3 Effects of drought on leaf rolling, days to 50% flowering and spikelet fertility

Leaf rolling of all the genotypes was affected by drought stress ranging from shallow V shaped leaves (score of 1) to leaf margins touching, 0-shape (6) (Figure 3.12). The mean leaf rolling score was 4 and genotypes were divided into two statistical groups. Group 1, genotypes with low leaf rolling score of 2 (Vandana, NERICA 2 and CT16323 -CA-25-M) and group II, genotypes with high leaf rolling score of 6 (NERICA 1, *Dourado precoce* and CT16333(1) CA-22-M). Leaf rolling score was lowest for the genotype Vandana (1.5) followed by CT16323 -CA-25-M and NERICA 2 both with a score of 2. The mean days to 50% flowering was 70 days ranging from 63 to 78 days. Vandana showed the earliest days to 50% flowering though this was not statistically different from NERICA 1 and CT16323 -CA-25-M. Drought stress delayed flowering of all the genotypes (Figure 3.13). The average delay in flowering was 5 days ranging from 1 to 8 days. CT16323 -CA-25-M had the shortest delay of 1 day followed by Vandana with a delay of 2 days. The longest delay in days to 50%

flowering of 8 days was observed in genotype *Duorado precoce* followed by NERICA 1 and CT16333(1) CA-22-M (7) The mean spikelet fertility was 61% ranging from 42 to 79% (Figure 3.14). Vandana once more showed the highest spikelet fertility of 79% followed by CT16323 -CA-25-M (70%) and NERICA 2 (66%). The overall mean relative spikelet fertility reduction was 34%. Vandana showed the lowest relative spikelet fertility reduction of 15% followed by CT16323 -CA-25-M (19%). The highest relative spikelet fertility reduction of 55% was observed in genotype *Duorado precoce*.

Table 3.12: Mean values of six early maturing genotypes evaluated under drought (Drt) and no drought (No Drt) conditions in October 2013 to February 2014 at KALRO Mtwapa Kenya

Genotypes	**Mean values**											
	LR†			RLWC			DFL			SF		
	Score			%			Days			%		
	NO DRT	DRT	Across	NO DRT	DRT	Across	NO DRT	DRT	Across	NO DRT	DRT	Across
NERICA 1	1	6.0	3.50	86.75	61.40	79.66	61	67	64	92.69	55.00	73.84
NERICA 2	1	2.0	1.50	87.50	69.20	78.37	67	71	69	92.23	66.10	79.18
Duorado	1	6.0	3.50	86.25	66.10	76.17	66	75	70	93.15	41.80	67.45
CT16333(1) CA-22-M	1	5.5	3.25	86.75	70.80	78.78	71	78	75	91.93	52.50	72.23
CT16323 -CA-25-M	1	2.0	1.50	87.25	70.30	78.77	61	63	62	87.05	70.00	78.51
Vandana	1	1.5	1.25	89.75	72.60	75.59	65	67	66	92.38	78.50	85.45
Mean	**1**	**3.8**	**2.42**	**87.38**	**68.40**	**77.89**	**65**	**70**	**68**	**91.57**	**60.60**	**76.11**
LSD (0.05)	**0**	**1.8**	**0.86**	**3.87**	**8.88**	**4.64**	**3**	**4**	**2**	**5.49**	**14.93**	**7.62**

†LR, Leaf rolling; RLWC, Relative leaf water content; DFL, Days to 50% flowering; SF, Spikelet fertility; NO DRT, no drought; DRT, drought

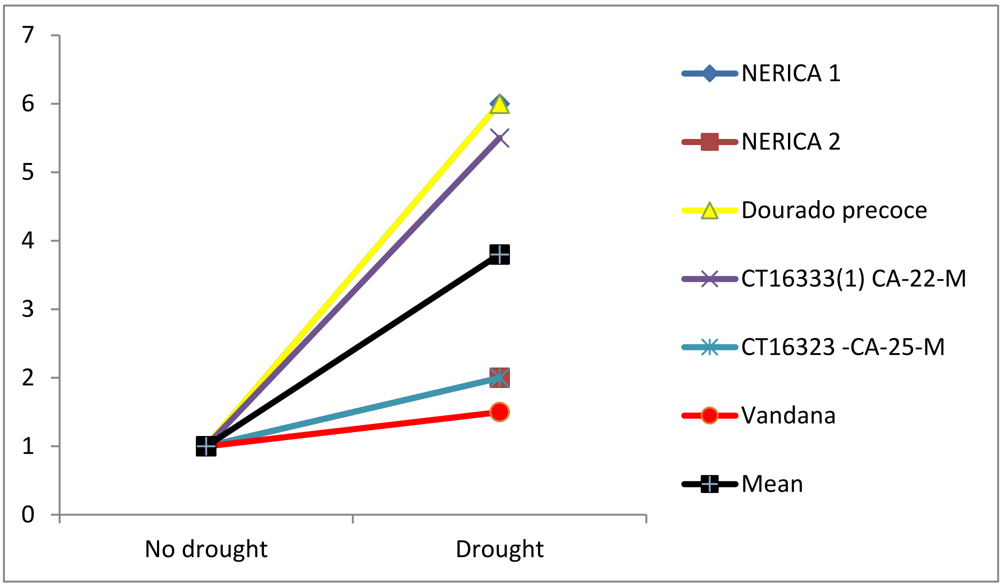

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Figure 3.12: Changes in leaf rolling of early maturing rice genotypes under drought and no drought conditions

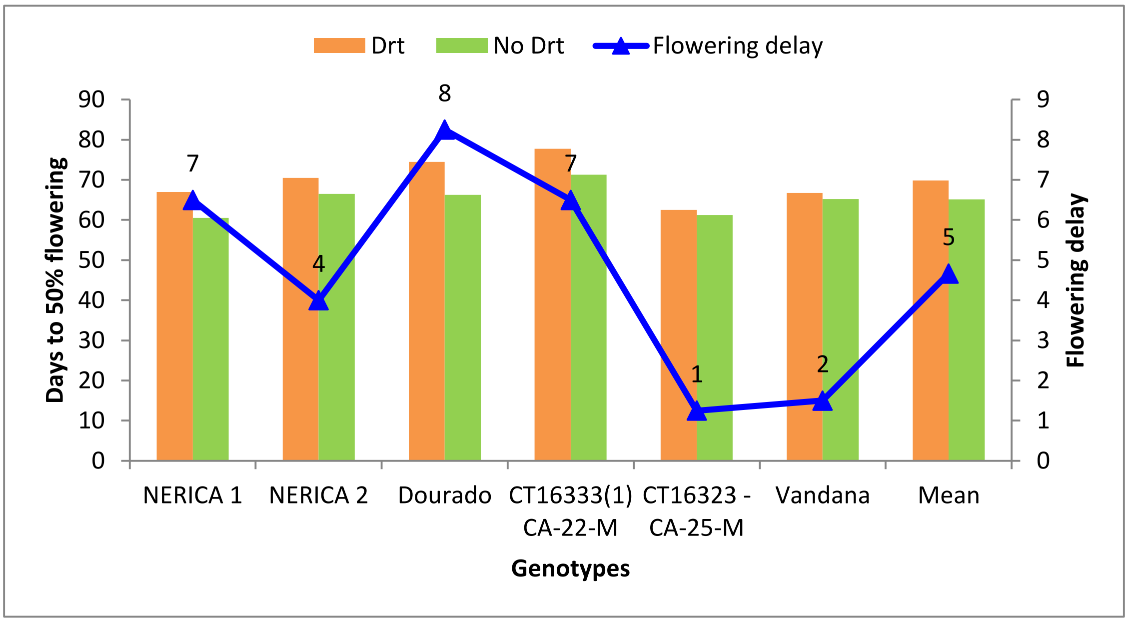

Figure 3.13: Flowering delay of early maturing rice genotypes under drought (Drt) and no drought (No Drt) conditions

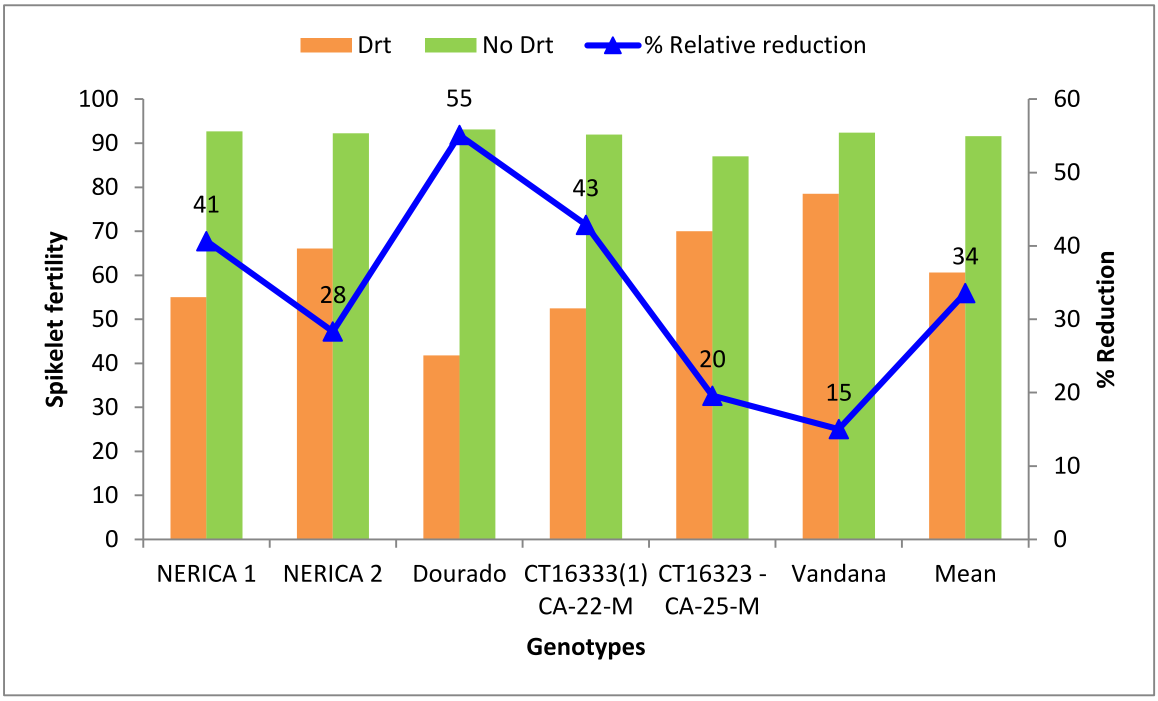

Figure 3.14: Relative spikelet fertility reduction of early maturing rice genotypes under drought (Drt) and no drought (No Drt) conditions

3.3.4.4 Selection index

The selection index was based on leaf rolling, days to 50% flowering and spikelet fertility. The traits were significantly associated and therefore weighted similarly (Table 3.13). Genotypes with negative values for leaf rolling and days to 50% flowering were more desirable. Vandana had the lowest negative index for leaf rolling (-3.03) followed by CT16323 -CA-25-M and NERICA 2. The rest of the genotypes showed positive indices. Days to 50% to flowering was most desirable for CT16323 -CA-25-M with an index of -1.33

Table 3.13: Weighted Indices and selection index based on leaf rolling, days to 50% flowering and spikelet fertility under drought conditions

Genotypes	**LR†**	**DFL**	**SF**	**SI**
NERICA 1	0.97	-0.53	-0.37	0.06
NERICA 2	-2.37	0.09	0.36	-1.92
Duorado	2.90	0.80	-1.25	2.45
CT16333(1) CA-22-M	2.24	1.38	-0.54	3.08
CT16323 -CA-25-M	-2.37	-1.33	0.62	-3.08
Vandana	-3.03	-0.58	1.19	-2.42

† LR, Leaf rolling; DFL, Days to 50% flowering; SF, Spikelet fertility; SI, Selection index

and least desirable for CT16333(1) CA-22-M (1.38). For spikelet fertility positive and larger values were more desirable. Once more Vandana had the highest index of 1.19 while *Duorado precoce* showed the lowest index of -1.25.

Overall the selection index values ranged from -3.08 to 3.08. The drought tolerant check was used for rating the other genotypes. Selection index for CT16323-CA-25-M (-3.08) was lower than that of Vandana and therefore identified as drought tolerant. Genotype NERICA 2 was identified as moderately drought tolerant while the rest of the genotypes were drought susceptible.

3.3.4.5 Association of characters

Association of characters was investigated under both drought and no drought conditions but only the results on association of characters under drought conditions were presented in Table 3.14. Under no drought conditions no significant differences were observed among the traits measured. Under drought conditions a significant and positive association was observed between leaf rolling and relative leaf water content (0.29*) and days to 50% flowering (0.49***). Spikelet fertility was significantly and negatively associated with leaf rolling (-0.65***) and days to 50% flowering (-0.53**). No significant associations were observed between relative leaf water content and days to 50% flowering and spikelet fertility.

Table 3.14: Phenotypic correlation coefficients of early maturing genotypes between leaf rolling, days to 50% flowering and spikelet fertility

Plant characteristics	**LR**	**DFL**
Leaf rolling (LR)		
Days to 50% flowering (DFL)	0.49***	
Percentage spikelet fertility (SF)	-0.65***	-0.53**

*, **, ***, Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively

3.4 Discussion

3.4.1 Weather and soil conditions

Drought screening for the medium to late maturing genotypes was imposed in January 2014 and beginning of February 2014 for early maturing genotypes. There was no rainfall received in January and the 13 mm of rainfall recorded in February were received towards end of the month. Thus the time of the year was conducive for drought screening. High temperatures (Maximum 31°C), low relative humidity and high wind speeds (average 145 and 129 miles per days in January and February were recorded during the time of drought screening. Evapotranspiration of crop plants is affected by vegetation properties as well as by solar radiation, temperature, wind speed, turbulence, relative humidity and soil properties among other factors (Blum, 2011). High wind speed increased the magnitude of evapotranspiration and evaporation from the soil media decreasing the available water for the rice plants. This partly explained why there was rapid drying of the soil media predisposing the plants to rapid soil moisture deficit.

The soil pH of the potting media was desirable for rice growth. The soil had low %N, hence inorganic N was applied to correct the deficiency. The potting media was mostly sandy with low organic matter signifying low water holding capacity another reason why the plants showed rapid wilting when drought was imposed.

3.4.2 Genotype performance of medium to late maturing genotypes under no drought in season I

The medium to late maturing genotypes evaluated under no drought conditions in season I differed significantly for phenology, morphology, grain yield and its related traits. Three local cultivars Tuliani, Supaa and Kibawa chekundu were found to be late maturing with days to 50% heading of more than 105 days. These three cultivars including Shingo la Mjakazi and Azucena were also tall (height of more than 140 cm) and low yielding. This confirms that indeed the popular local cultivars currently grown by farmers in the coastal lowlands of Kenya are late maturing and low yielding. However, the results revealed that cultivars such as Tuliani and Supaa had higher number of grains per panicle and heavy grains as indicated by higher thousand grain weight of 30 g and above. This indicated that these genotypes may be used as donors of big panicles and heavy grains. Moreover farmers have continued to use these local varieties because of their good grain quality. Except for CT16333(1)-CA-22 which did not fit in the medium maturing group and was therefore, evaluated for drought tolerance together with the early maturing genotypes in the second season, all the other exotic genotypes were found to be medium maturing. Among these, four genotypes LUYIN 46, IR10L151, IR74371-54-1-1, and IR55423-01 were found to be high yielding and therefore candidates for further evaluation in the field.

3.4.3 Genotypic performance under drought and no drought in season II

Within the medium to late maturing group and the early maturing group, no variation was observed among genotypes for all physiological traits measured under no drought conditions. However, under drought conditions, genotypes varied significantly for canopy temperature, leaf rolling and leaf drying, indicating that physiological traits measured in this study were expressed under drought stress conditions only and therefore, important indicators of drought in screening trials. Variation in physiological response to water stress at reproductive stage among rice genotypes has been reported for leaf rolling and death (Lilley and Fukai, 1994; Pantuwan *et al.*, 2002; Kumar *et al.*, 2014), canopy temperature (Garrity and O'Toole 1995) and for relative leaf water content (Bimpong *et al.*, 2011; Kumar *et al.*, 2014).

3.4.4 Effects of drought stress

The drought tolerance index assisted in the determination of the extent of the effect of drought stress on the genotypes relative to the no drought conditions. It was also preferred to the raw values for comparing genotypes. The surface temperature of the canopy is related to the amount of transpiration resulting in evaporative cooling. Warmer temperatures result to stomatal closure, low transpiration and reduced transpiration cooling (Blum 2011). In this study, changes in canopy temperature varied among the genotypes. Genotypes with low canopy temperature maintained greater transpiration rates under stress conditions while genotypes with high canopy temperatures experienced low transpiration rates under stress conditions. Canopy temperature of Kitumbo, a local traditional cultivar was the least affected by drought indicating that this genotype may be drought tolerant. NERICA-L-25 experienced the highest increase in relative canopy temperature indicating that this genotype had high stomatal closure and low transpiration rate under drought stress hence highly drought sensitive. Canopy temperature is an indirect measure of internal water status and important predictor of yield performance under drought. Garrity and O'Toole (1995) found this trait to be very effective for field screening for drought avoidance phenotyping in rice.

Relative leaf water content (RLWC) estimates the volumetric water content of the leaf tissue relative to its capacity at full turgidity; it could be regarded as a measure of water deficit in the plant leaf (Blum, 2011). The average levels of relative leaf water content of 58% observed in this study under drought conditions indicated pronounced levels of leaf wilting. Other researchers have also reported similar levels in their studies (Bimpong *et al.*, 2011; Kumar *et al.*, 2014). Remarkable reduction in relative leaf water content under drought stress relative to the control was observed and was more pronounced for NERICA-L-25. The pronounced drought effects recorded for NERICA-L-25 may have been caused by the warmer temperatures observed in this genotype under drought conditions. Shingo la Mjakazi and the drought tolerant check (IR74371-54-1-1) showed the lowest relative reduction in relative leaf water content indicating that these genotypes were less affected by drought compared to the other genotypes and therefore possibly drought tolerant.

Leaf rolling is a well-recognized dehydration symptom extensively used by breeders in selecting for avoidance of water stress in rice (O'Toole and Cruz, 1980; Blum, 2011). Among the medium to late maturing genotypes leaf rolling and death were more pronounced among genotypes that showed higher percentages of relative increased canopy temperature and reduced relative leaf water content. These genotypes were also larger in plant size which may have resulted in more transpiration demand predisposing the genotypes to more water stress. In both experiments, leaves of the drought tolerant checks IR74371-54-1-1 and Vandana rolled slightly confirming their potential to tolerate water stress at reproductive growth stage.

Flowering delay is an expression of drought susceptibility. The mean delay in flowering was eight days for the medium to late maturing group and five days for the early maturing group. Similar delays in flowering have been found by other researchers (Lilley and Fukai, 1994). Among the medium to late maturing genotypes, delayed flowering was not observed in genotype IR74371-54-1 confirming that this genotype had high reproductive stage drought tolerance. The genotype NERICA-L-25 had the longest delay of 15 days indicating that the genotype was drought susceptible. A delay in flowering observed in NERICA-L-25 may have been predisposed by higher canopy temperature and low relative water content. Among the early maturing genotypes, CT16323-CA-25-M had the shortest delay of 1 day followed by Vandana with a delay of two days indicating that these genotypes were drought tolerant.

Grain yield reduction by stress is a measure of the severity of drought stress and genotype resistance in terms of absolute yield under stress. In this study the mean relative yield reduction under drought compared with the irrigated control was 58%. The intensity of stress observed in this study was similar to that observed in other studies under moderate stress at reproductive stage (Lilley and Fukai, 1994b; Kumar *et al.*, 2009; Verulkar *et al.*, 2010). Stress severity varied among the genotypes. Relative yield reduction (RYR) was mild in IR74371-54-1 (31%) and severe in genotypes NERICA-L-25 and FKR19 each with RYR% of 79%. Spikelet fertility is the main yield component affected when stress occurs during the reproductive stage because it leads to irreversible processes of yield reduction (Ekanayake *et al.*, 1989; Lafitte *et al.*, 2003). The severity of drought observed in both experiments resulted in significant reduction in spikelet fertility. High spikelet sterility resulted from retention of mature spikelets inside the flag leaf sheath prohibiting the opening of spikelets. White and discoloured empty spikelet's were also observed in genotypes such as Bas370, NERICA-L-25, FKR19, NERICA 1, *Dourado precoce* and CT16333(1)CA-22-M indicating that these genotypes were drought sensitive. Furthermore these genotypes showed high relative spikelet fertility reduction of more than 50%. In rice, flowering is delayed under stress and the extent of delay is a function of the stress level and genotype. Delayed flowering is an expression of drought susceptibility. In this study, delay in flowering of drought tolerant lines was significantly lower than that in susceptible lines. Genotypes NERICA-L-25 and FKR19 showed prolonged delay in flowering indicating that these genotypes were probably drought susceptible.

3.4.5 Selection index

Because of the complexity of drought tolerance trait involving complex interactions of biochemical, physiological and morphological characteristics (Efisue *et al.*, 2009), a selection index in which it is assumed that genotypic selection based on integrated characters is superior to selection based on a single character is used to identify drought tolerant and susceptible genotypes (Garrity and O'Toole, 1994; Bänziger *et al.*, 2000). A selection index may either combine information on secondary traits with grain yield or on secondary traits alone, to give one value for drought tolerance (Bänziger *et al.*, 2000). Among the medium to late maturing group, the selection index revealed that the highly drought tolerant check (IR74371-54-1-1) was exceptional with a SI of -6.68 and therefore rated highly tolerant. Shingo la Mjakazi and Kitumbo fell in the same class with the moderately tolerant check and were rated moderately tolerant. Genotypes NERICA-L-25, Tuliani and Kibawa Chekundu were found to be highly susceptible. Among the early maturing cultivars selection index for CT16323-CA-25-M (-3.08) was lower than that of Vandana and therefore identified as drought tolerant. Genotype NERICA 2 was identified as moderately drought tolerant while the rest of the genotypes were drought susceptible.

3.4.6 Association among traits

Correlation analysis is used as one of the tools for determining the value of other plant characteristics in relation to grain yield. In this study the relationship between grain yield per plant and physiological traits measured was significant under drought conditions but not under no drought conditions. Results from various studies have also reported that low canopy temperature, leaf rolling and drying scores was related to better yield or yield stability under drought stress (Ingram *et al.*, 1990; Garrity and O'Toole, 1995). Spikelet fertility was the highest contributing factor to grain yield per plant under drought conditions. These finding are similar to those revealed by other researchers (Garrity and O'Toole, 1994; Zou *et al.*, 2005) and suggest. spikelet fertility is the main yield component affected when stress occurs during the reproductive stage (Ekanayake *et al.*, 1989; Lafitte *et al.*, 2003). Therefore more emphasis should be put on spikelet fertility under drought stress for a drought breeding programme. Traits correlated with spikelet fertility if identified can be used to indirectly improve grain yield. In this study all the physiological traits were significantly correlated with spikelet fertility. The best approach to indirectly select for increased grain yield in these materials was to select for higher spikelet fertility, high RLWC, low canopy temperatures, reduced leaf rolling and leaf drying scores.

3.5 Conclusions

This study has shown that genotypes varied significantly in grain yield per plant, spikelet fertility and days to 50% flowering under drought and no drought conditions and in drought related physiological traits under drought conditions. The drought tolerance index was useful in determining the effect of drought stress on each genotype and showed that genotypes performed differently in response to drought stress. The drought tolerance index should be useful in breeding rice for drought tolerance. The selection index was found to be useful in identifying drought tolerant and susceptible genotypes. Among the medium to late maturing group two local cultivars namely, Shingo la Mjakazi and Kitumbo were found to be moderately drought tolerant while among the early maturing group, CT16323-CA-25-M performed better than drought tolerant check Vandana while NERICA 2 was probably moderately drought tolerant. Inclusion of checks with known tolerance to drought stress was found to be effective in rating those genotypes whose level of drought tolerance was unknown. Spikelet fertility was correlated with grain yield and the other physiological traits under stress. Breeders may use this trait in combination with other physiological traits to indirectly select for grain yield under drought conditions. The study also confirmed that the popular local cultivars currently grown by farmers in the coastal lowlands of Kenya were tall, late maturing and low yielding. However, cultivars such as Tuliani and Supaa had higher number of grains per panicle and heavy grains and may be used as donors for these traits.

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Chapter Four

Inheritance of earliness in interspecific and *Oryza sativa* L. rice lines under drought and no drought conditions

Abstract

The drought escape trait is an important yield component in areas where drought is severe, predictable, and terminal. Knowledge of combining ability of short to medium duration rice cultivars would be beneficial in setting breeding strategies for development of early maturing cultivars for the long and short rain seasons in the coastal region of Kenya. The objective of this study was therefore to investigate inheritance of earliness and combining ability of days to antheis and maturity and some morphological traits in rice. Five interspecific and five *Oryza sativa* L. rice lines were mated in a half diallel mating design and F_1 progenies advanced to F_3 generation. The 45 F_3 populations, 10 parents and one check were evaluated in 7 x 8 alpha lattice design with two replications under three no drought and one random managed drought stress condition at three sites in coastal region of Kenya. Traits measured were days to heading, days to anthesis, days to maturity, number of productive tillers per plant and plant height. There was significant variation ($p<0.001$) among genotypes for all the traits measured. The F_3 populations CT16323-CA-25-M x Vandana (E x E) and NERICA 1 x Vandana (E x E) were found to be extra early and consistently showed shorter days to heading under no drought and drought conditions. Across environments, general combining ability (GCA) and specific combining ability (SCA) effects were highly significant ($P<0.01$) to significant ($P<0.05$) all traits measured. Inheritance of earliness based on days to heading was conditioned by non-additive gene action under drought conditions, and additive gene action under no drought conditions. This was also observed for days to anthesis and plant height. For days to maturity and number of productive tillers per plant, additive gene action was more important under drought and no drought conditions. Therefore, improvement of earliness can be done under no drought conditions through recurrent selection strategy. One interspecific line CT16323-CA-25-M and one *Oryza sativa* line, Vandana, consistently exhibited negative general combining ability for phenology, under drought and no drought conditions which was desirable. These lines could be used as sources for earliness in rice breeding programmes in sub-Saharan Africa. Vandana combined earliness with desirable general combining ability for increased number of productive tillers per plant and plant height. The best specific combinations were populations CT16323-CA-25-M x Vandana and *Duorado* x Vandana which combined short duration with increased plant height and higher number of productive tillers per plant. Early generation testing in these crosses can be employed to identify plants with desirable characters thus reducing the breeding load.

Keywords: Drought escape, gene action, general combining ability, earliness, phenology, rice, specific combining ability

4.1 Introduction

Drought escape relates to short duration or early maturing genotypes that escape effects of water stress through synchronisation between plant phenology and a given profile of drought (Blum, 1982). In rice, the drought escape trait has been extensively used in areas where drought is severe, predictable, and terminal (Fukai and Cooper, 1995; Jongdee *et al.*, 2006). According to Jongdee *et al.* (2006), severe drought occurring late in the season can cause 45–50% yield loss. Under these conditions, selection for early maturing varieties greatly improves grain yield because cultivars that flower early tend to have greater numbers of fertile spikelets than those that flower late in the season (Mackill *et al.*, 1996). Although the coastal lowlands of Kenya experience a bimodal type of rainfall, farmers have been forced to raise only a single rice crop during the long rain season, skipping the short rain season due to lack of short duration cultivars suitable for the season. Therefore, it would be practical to breed for high yielding, short duration cultivars with desired plant height that can be grown in both the long rain and short rain season in the region.

An effective breeding strategy is preceded by the gathering of information on the nature and magnitude of inheritance for the desired traits in a given set of materials. The diallel analysis technique has been used extensively to understand gene action involved in the expression of quantitative characters (Baker, 1978). Estimation of gene action through variance component approach involves estimating genetic components of variances and defining them in terms of gene action (Hallauer *et al.*, 1988). General combining ability (GCA) is associated with additive gene effects, whereas specific combining ability (SCA) is associated with non-additive gene effects (Sprague and Tatum, 1942; Falconer, 1989).The additive genetic variance is the chief cause of resemblance between relatives and therefore determines responsiveness of a population to selection (Sleper and Poehlman, 2006).

Studies on inheritance of phenological and morphological traits in rice have mostly been based on direct analysis of genetic parameters (Dwivedi *et al.*, 1980; Chen *et al.*, 2006) and on GCA and SCA variances in diallel tables (Manickavelu *et al.*, 2006; Abd Allah *et al.*, 2009; Malarvizhi *et al.*, 2010; Muthuramu *et al.*, 2010; Dwivedi and Pandey, 2012). For phenological traits additive gene action has been reported to play a major role in conditioning inheritance of earliness (Li and Chang, 1970). Another study reported that non-additive gene action was more important than additive gene action contributing 68% of the total genetic variation of heading date (Chen *et al.*, 2006). In yet another study, Dwivedi and Pandey (2012) reported that both additive and non-additive gene action were important in inheritance of days to flowering. On morphological traits, additive gene action has been reported to play a major role in conditioning inheritance of plant height contributing 55 to

60% of the total genetic variance (Abd Allah *et al.*, 2009; Muthuramu *et al.*, 2010). Furthermore, among interspecific progenies evaluated under stress and non-stress environments, Efisue *et al.* (2009) reported the importance of additive gene action for tiller number and plant height, while Lamo (2009) showed that both additive and non-additive effects were important for these traits. These studies suggest that breeding schemes designed to make use of both additive and non-additive gene action are most suitable in developing cultivars with desired phenological and morphological traits for the local environment.

The African Rice Centre (ARC) and the International Centre for Tropical Agriculture (CIAT) have made considerable progress in developing early maturing interspecific lines while materials from the International Rice Research Institute (IRRI) are cosmopolitan mostly because of their high yield potential. A few of these materials have been introduced in Kenya and some adopted in the region. However, information on the genetic qualities of these materials including the local cultivars, which is useful in selection and development of new germplasm is lacking. To accelerate the development of high yielding, short duration cultivars with desired plant height for the region, it is important to determine the usefulness of these lines in combining ability studies. Therefore, the objective of this study was to investigate a) inheritance of earliness; and b) combining ability of phenological and some morphological traits in selected interspecific and *Oryza sativa* L. pure lines and their crosses.

4.2 Materials and methods

4.2.1 Description of study sites

The study was conducted on-station at Kenya Agricultural and Livestock Research Organisation (KALRO)-Mtwapa and KALRO-Matuga and on farm at Msambweni sub-county of Kwale county. KALRO-Mtwapa is located 20 km north of Mombasa in Kilifi south county, along Mombasa-Malindi road. It lies on latitude 3°50’S and longitude 39°44’E at an elevation of 15 m above sea level (masl). Annual mean temperatures are between 22^{o}C and 26^{o}C. The area receives bimodal mean rainfall of about 1200 mm with reliable long rains of 600 mm falling mid-March to July and the variable short rains of 250 mm falling in mid-October to December. The soils are dominated by orthic acrisols (80% sand) with low inherent fertility (Jaetzold and Schmidt, 1983). KALRO Matuga is situated 15 km south of Mombasa from the Likoni ferry in Kwale county. The site is at Latitude 4°9‘S and Longitude 39°34‘E at an elevation of 132 masl. Annual mean temperatures are between 24^{o}C and 26^{o}C. The area receives bimodal mean annual rainfall of about 1200 mm with the long rain season of 750mm and short rain season of 350 mm. The soils are derived from Pliocene sandstones and are commonly referred to as Magarini sands (Jaetzold and Schmidt, 1983). They are low in C, N, P, K and are moderately acidic (Jaetzold and Schmidt, 1983). The typical agro-ecological zonation for KARLO-Mtwapa and Matuga is coastal lowland three (CL3-coconut cassava zone). In these two sites the experiments were evaluated during the short rain season and represented no drought conditions under upland ecology.

The Msambweni on-farm site is 50 km south of Mombasa from Likoni ferry. The site is at Latitude 4°28'S and Longitude 39°29'E at an elevation of about 19 masl and lies in coastal lowlands 2, (CL2), classified as the coastal lowlands sugarcane zone and occurs as a pocket in Ramisi area in Kwale county and is the wettest zone. The annual minimum and maximum temperatures range from 19^{o}C to 24^{o}C. Rainfall in this zone is bimodal ranging from 1200 to 1400 mm annually. The long rain season of 800 mm falls between March to August and short rain season of 400 mm falls between mid-October to December (Jaetzold and Schmidt, 1983). Msambweni, represented lowland ecology and the experiments were planted during the short and long rain season. The short rain season represented random managed stress while the long rain season represented no drought condition.

4.2.2 Germplasm: Parents and crosses

The lines used in this study consisted of five O*ryza sativa* L. and five interspecific rice pure lines drawn from the African-Rice Centre (ARC), the International Centre for Tropical Agriculture (CIAT) and the International Rice Research Institute (IRRI). They represented three maturity groups; five early, two early to medium and three medium maturing. Drought tolerance levels at reproductive stage also differed among the lines; three had high drought tolerance, two were moderately drought tolerant while five were drought susceptible. All lines can be grown under rainfed upland and lowland ecosystem except for NERICA-L-25 which is purely suitable for the rainfed lowland ecology. More information on the characteristics of these lines is given in Table 4.1.

Table 4.1: Source and characteristics of ten diallel parents used in the study

Genotype	***Source**	**Maturity group**	**Other Characteristics**
***Interspecific* lines**			
NERICA 1	ARC	Early	Aromatic, tolerant to lodge, blast and insects (Kimani *et al.*, 2013)
NERICA 2	ARC	Early	Slightly tolerant to drought (Sikuku *et al.*, 2010)
CT16323-CA-25-M	CIAT	Early	Drought tolerance, low yielding, good grain quality (Kimani, 2010)
CT16333(1)-CA-22-M	CIAT	Early to Medium	Good grain quality, tolerant to low soil N and P (Kimani, 2010)
NERICA-L-25	ARC	Medium	Drought susceptible, high yielding (Musila, Unpublished)
***Oryza sativa* L. lines**			
Vandana	IRRI	Early	High reproductive stage drought tolerance, low yielding (Venuprasad *et al.*, 2007)
Dourado precoce	Kenya	Early	Local adapted cultivar with good grain quality but low yielding (Kimani *et al.*, 2013)
IR74371-54-1-1	IRRI	Early to medium	High reproductive stage drought tolerance, high yielding (Verulkar *et al.*, 2010)
Luyin 46	IRRI	Medium	Drought susceptible, high yielding (Musila, Unpublished)
IR55423-01	IRRI	Medium	Moderate reproductive stage drought tolerance, high yielding, (Venuprasad *et al.*, 2007)

*IRRI-International Rice Research Institute; CIAT-International Center for Tropical Agriculture; ARC-Africa Rice Centre (WARDA)

4.2.3 Generation of crosses

The 10 lines were crossed in a half diallel mating design. Crosses were performed at Kenya Agricultural and Livestock Research Organization (KALRO-Mtwapa. Plants were sheltered in a 4 x 7 m wooden screen house. The roof of the screen house was covered with a transparent polyethylene cover and a black shade net. This was done to shelter the emasculated and pollinated panicles from wind, rain, direct sunlight and to optimise the temperatures for flowering and seed set. Sides were covered with a green shade net to allow maximum light penetration and keep away insects and pests. The parents were planted in black polyethylene pots with 25 cm internal diameter and 30 cm height. Each pot was filled with 18 kg of upland soil. To synchronize flowering, planting was staggered on three dates;

21st January, 11th February and 5th March 2013. Pots were watered to field capacity before planting. Thereafter optimum conditions were ensured to avoid water stress. Diamonium phosphate (DAP) fertilizer was applied in the pots during planting at recommended rate of 60 kg P ha^{-1}. Top dressing was done using calcium ammonium nitrate (CAN) fertilizer at the rate of 120 kg N ha^{-1} applied in three splits of 40 kg ha^{-1}; at 21 days after transplanting, tillering stage and at panicle initiation stage. Rice stem borer was effectively controlled using a synthetic pyrethroid. Weeds were controlled by hand picking.

Emasculation was done from 6.00 am to 8.00 am. Good looking female panicles that had emerged 5 to 10 cm from the leaf sheath were selected for emasculation. Using a sharp pointed small pair of scissors, the upper and lower spikelets were removed leaving the middle part. The palea and lemma of the selected spikelets were cut at the middle in order to expose the anthers. Anthers were safely removed using a pair of forceps. Immediately after emasculation the panicle was covered with a 42 x 170 mm ice cream poly bags to protect it from unwanted foreign pollen and labelled with its female parent name and date of emasculation. Pollination commenced from 10.00 am to 1.00 pm the time during which maximum anther dehiscence was observed. Method of pollination was the approach method in which the pot containing the male parent with the blooming panicle was carried to the emasculated female panicle and placed beside it. The ice cream poly bag covering the emasculated panicle was lifted and the male blooming panicle was carefully positioned above the female panicle. The two culms of both parents were covered with a glassine bag and fastened together with an office clip. Adequate pollination was ensured by tapping the glassine bag after every 10 to 15 minutes. After pollination the female panicle was covered with the ice cream poly bag to prevent desiccation of the pollinated panicle. On the label the name of the male parent and date of pollination was added. Seven days after pollination holes were made on the ice cream polybag to lower the temperatures and prevent accumulation of excessive humidity inside the bag. This allowed normal development of the F_1 seed. A few days after crossing, ovule could be seen on successful crosses. Mature seeds were harvested when they lost their green colour between 25 to 30 days after pollination. Seeds from each female panicle were harvested separately and stored in well labelled white medical envelopes. The label for each cross was also inserted inside the envelope for identification. The seed set realized were few to establish a field trial in most of the crosses; hence the F_1s were advanced to F_3 populations.

4.2.4 Experimental design

The resulting 45 F_1s generated using half diallel mating design, were advanced to F_3 populations using the bulk population method. The experimental materials consisted of 56 treatments (entries) including the 45 F_3 populations, 10 parents and 1 check. Experimental design was 7 x 8 alpha lattice with two replications.

4.2.5 Experiments

4.2.5.1 Managed drought experiment

The managed drought stress experiment was established on station at KALRO-Matuga during the short rain season under upland ecology. However, immediately after transplanting there was water shortage which did not allow the running of the drought and no drought experiments concurrently. Due to this less than 50% of the plants survived and therefore no data was collected from this experiment.

4.2.5.2 Random drought stress experiment

The random drought stress during the rain experiment was planted on farm at Msambweni during the short rain season. It was established under rainfed lowland ecology. It was planted in mid-October 2014 and the last rainfall of 44 mm was received 65 days after planting. Random drought stress occurred during the reproductive stage from the panicle initiation stage to harvesting.

NB: Random drought stress is meant to mean unpredictable drought occurring at the middle of the rain season or premature termination of the rain season due to adverse weather conditions resulting to terminal drought.

4.2.5.3 No drought stress experiments

The no drought stress experiments included two experiments established on station at KALRO-Matuga and KALRO-Mtwapa during the short rain season under upland ecology and one established on farm at Msambweni during the long rain season under lowland ecology. The KALRO-Matuga experiment was planted mid-October 2014 and received supplemental irrigation water since rainfall during the short rain season was not adequate. At Mtwapa the experiment was established in December 2014. Plants were planted in an open field in black polyethylene pots with 25 cm internal diameter and 30 cm height. The Msambweni site was planted in April 2015 and was purely rainfed since the rainfall was adequate.

4.2.6 Management of experiments

Under field conditions, at KALRO-Matuga and Msambweni, the fields were un-flooded and aerobic conditions. The experimental plot were 3.2 m^2 with inter- and intra- row spacing of 20 cm to give a total of 80 plants per plot. Seed for each entry was first grown in plastic containers and transplanted to the field on the 12th day. Two seedlings were transplanted and later thinned to one seedling per hill. At KALRO-Mtwapa, each pot was filled with 20 kg of upland soil. Pots were watered to field capacity before planting. Five seedlings per pot were transplanted and there were five plants per pot spaced at 10 cm each. Each entry was assigned eight pots to give a total of 40 plants per entry. From transplanting to dough stage each pot received one and half liters of water each in the morning hours on daily basis and by the end of the day there was no standing water in each pot. Thereafter, watering was done after every two days to allow the plants to dry up for harvesting.

The overall management was application of basal inorganic fertilizers; calcium ammonium nitrate (CAN) as a source of N and diamonium phosphate (DAP) as a source of P. The P was applied during planting at recommended rate of 60 kg P ha^{-1}. The N was top dressed at the rate of 120kg N ha^{-1} applied in three splits of 40 kg ha^{-1} at 21 days after transplanting, tillering stage and at panicle initiation stage. Source of micro nutrients was foliar feed which was sprayed once during the tillering stage. Rice stem borer was effectively controlled using a synthetic pyrethroid. Weeds were controlled by hand picking. Harvesting was carried out manually.

4.2.7 Soil sampling

At KALRO-Matuga and Msambweni, the soil was sampled in the 0-20 cm top soil layer over the experimental block. A graduated soil auger was used for sampling the soil in both diagonals at the four corners, at the middle, then between the corners, and between the middle of diagonals and corners making a total of 17 samples. At KALRO-Mtwapa, 15 samples were collected from 15 planting pots. For each site samples were bulked to form a composite and two sub-samples were taken per composite, thus, a total of six samples were submitted for analysis at NARL (National Agricultural Research Laboratories) soil analytical laboratories.

4.2.8 Rainfall data

Rainfall data were recorded from the nearest meteorological station (Table 4.3). For Mtwapa site this was Mtwapa meteorological weather station located 60 m from the experiment, Matuga site, it was from Matuga weather station about 10 m from the site. While for Msambweni data was obtained from Msambweni meteorological weather station.

4.2.9 Data collection

The standard evaluation system (SES) for rice reference manual (IRRI, 1996) was used for all traits measured except where stated. From each plot (entry), thirty six plants were randomly selected and tagged for data collection. On each plant, data were collected on days to heading (DH), days to flowering (DFL), days to maturity (DM), plant height (PHT) and number of productive tillers per plant (TNO). Days to heading were determined visually when the tillers per plant had panicles exerted. Days to flowering were determined visually when tillers per plant had anthers exerted. Days to maturity were recorded as the number of days from planting to when 85% of the panicles in a plant were mature. Plant height was measured at maturity stage using a calibrated meter scale from soil surface to tip of the tallest panicle (awns excluded). Number of productive tillers per plant was recorded by counting the number of productive tillers per hill.

In this study, earliness was based on days to heading since it is a key determinant of physiological maturity of rice (Jiang *et al.*, 2007).

4.2.10 Data analysis

Analyses of variance per environment and across environments were conducted using PROC GLM in SAS (SAS Institute, 2012), where parents were considered fixed effects and environments and replications and blocks within replications as random effects. General combining ability (GCA) effects of the parents and specific combining ability (SCA) effects of the crosses as well as their mean squares at each environment and across environments were estimated following Griffing's method 2 for the diallel formed by P parents and their P(P-1)/2 F1s. Parents were considered as fixed effects (model 1) in the test of significance (Griffing, 1956). Diallel analysis was done using the DIALLEL-SAS program (Zhang *et al.*, 2005) according to the following linear model for individual environment: $X_{ijk} = \mu + r_k + g_i + g_j + s_{ij} + p_{ijk}$, where Xijk = Observed measurement of the parent (i = j) or cross between ith and jth genotypes in the kth replicate; μ = the population mean; rk = the replication effect; gi = the GCA effect for the ith parent; gj = the GCA effect for the jth parent; sij = the SCA effect for the cross between ith and jth parent with sij = sji; pijk =experimental error. The interaction terms were used to test for the significance of the corresponding main effects.

The environments and replications within environments were considered random effects and therefore tested against the residual error term.

The relative importance of GCA and SCA were estimated using the general predicted ratio (GPR) for the traits observed (Baker, 1978). The ratio was estimated as follows; $2\sigma^2$GCA/($2\sigma^2$GCA + σ^2SCA) where $2\sigma^2$GCA and σ^2SCA are the variance components for GCA and SCA, respectively estimated from Griffing's method 2 model II (random effects). Ratios close to one indicate additive effects are important in the inheritance of the trait while ratios close to zero indicate dominance and epistasis effects are important in the inheritance of the trait.

4.3 Results

4.3.1 Soil chemical properties

The soil pH was satisfactory for rice growth at KALRO-Matuga and Mtwapa but slightly alkaline at Msambweni though not to detrimental levels for rice growth. Nitrogen and organic matter were found to be deficient in all the sites. Phosphorus and potassium were found to be low for rice growth at Matuga and Msambweni, while calcium was inadequate at all the sites. The soils had high percentage of sand and low percentages of clay and silt contributing to extremely low cation exchange capacity (CEC). More details for soil properties for each site are given in Table 4.2.

Table 4.2: Soil properties for the study sites

Parameter	**Mtwapa**		**Matuga**		**Msambweni**	
	Value	**Class**	**Value**	**Class**	**Value**	**Class**
Soil pH	7.34	satisfactory	6.50	satisfactory	7.69	moderately alkaline
Organic Matter %	0.97	very low	0.44	very low	0.81	very low
Total N %	0.10	low	0.05	Low	0.08	low
Phosphorus ppm‡	34	adequate	15	Low	6	very low
Potassium ppm	156	adequate	86	Low	31	low
Calcium ppm	700	low	700	Low	580	low
Zinc ppm	12.60	high	2	adequate	1.52	adequate
Magnesium ppm	180.29	high	157.30	High	222.64	high
CEC†	12.80	low	7.60	very low	8.40	very low
Sand%	78		86		88	
Silt%	8		0		4	
Clay%	14		14		8	
Soil texture	Sandy loam		sandy loam		sandy loam	

‡ppm, parts per million; † CEC, cation exchange capacity

4.3.2 Rainfall data

The short rain season occurred between October and December (Table 4.3). Most of it fell in October at Matuga and Mtwapa and in November at Msambweni. The long rain season occurred between April to August with most of it falling in May. A drastic reduction of 213 mm of rainfall was observed from June onwards.

Table 4.3: Rainfall data in the test sites during the period of study

Season	Rainfall	October 2014	November 2014	December 2014	January 2015	February 2015	March 2015
Short rain	KARLO-Matuga						
	Total rainfall (mm)	186.5	147.8	88.1	0	0	-
	No. of rainy days	5	4	2	0	0	-
	KARLO-Mtwapa						
	Total rainfall (mm)	190.2	110	93	0	0	83.7
	No. of rainy days	10	15	2	0	0	4
	Msambweni short rain season						
	Total rainfall (mm)	105	166	119.5	0	0	-
	No. of rainy days	7	5	2	0	0	-
Long rain	Msambweni long rain season						
		April	**May**	**June**	**July**	**August**	**September**
	Total rainfall (mm)	115	298	85.5	80	75.5	0
	No. of rainy days	8	20	6	8	5	0

4.3.3 Average performance of F$_3$ progenies and their parents

4.3.3.1 Across no drought stress

The check was found to be late maturing and therefore was eliminated from the analysis. Generally the materials planted at Mtwapa took a longer time (83 days) to reach days to heading while shorter time was observed at Msambweni during the long rain season (72 days) (Table 4.4). The same trend was observed for days to anthesis and days to maturity. The highest mean number of productive tillers per plant of 11 was observed at Msambweni and ranged from 7 to 16 productive tillers per plant. Mtwapa showed the lowest mean number of productive tillers per plant of 7 ranging from 5 to 10 productive tillers per plant. Matuga showed the shortest average plant height of 93 cm while at Msambweni, plants were tall showing a mean plant height of 108 cm. Across environments, the earliest populations with the shortest days to heading were crosses between E x E (early x early), CT16323-CA-25-M x Vandana (70 days) followed by NERICA 1 x Vandana (71 days). Two early maturing parents NERICA 1 and CT16323-CA-25-M dominated the early class. The early class was dominated by crosses between E x E, and E x EM (early x early to medium). In addition, the majority of the crosses were between interspecific x *Oryza sativa* and interspecific x interspecific. The latest maturing population was Luyin 46 x IR74371-54-1-1 with 92 days to heading. The late maturing populations were mostly crosses between M x M (medium x medium) and M x EM (medium x early medium) and the common parents were medium maturing parents NERICA-L-25 and IR55423-01. Number of productive tillers per plant of the selected early maturing populations was low (5 to 9 tillers) while plant height was intermediate (90 to 125 cm).

4.3.3.2 Random managed drought stress

Under random managed drought stress in Msambweni, the average days to heading was 75 days (Table 4.5). Compared to the no drought stress environment on the same site during long rain season, there was a mean delay in flowering of three days and a mean delay in maturity of 5 days. The mean number of productive tillers per plant was 9 and mean plant height was 102 cm. The population *Duorado* x IR74371-54-1-1 showed the earliest days to heading of 66 days maturing statistically earlier than parent IR74371-54-1-1. Other populations showing shorter days to heading of less than 70 days were CT16323-CA-25-M x IR55423-01, CT16323-CA-25-M x IR74371-54-1-1, and NERICA 1 x Vandana. The early class was dominated by crosses between E x E, E x EM and E x M and *vice versa*. Sixty percent of the early maturing populations were between interspecific and *Oryza sativa* lines. Vandana, an early maturing line, was the common parent appearing in 40% of the selected early maturing populations. The population, Vandana x IR74371-54-1-1, combined earliness with higher number of productive tillers per plant of 11. The latest population was Luyin 46 x IR55423-01 (M x M) with 88 days to heading. Once more, the latest maturing populations were mostly crosses between M x M and M x EM and the common parent was IR55423-01 (M). Low (5 to 9 tillers) number of productive tillers per plant was observed for most of the populations. Plant height was mainly intermediate with populations CT16323-CA-25-M x Vandana (E x E) and *Duorado* x Vandana (E x E) having the tallest plants of 118 and 120 cm, respectively.

4.3.3.3 Across environments

The average days to heading across the no drought and the random drought environments was 77 days ranging from 70 to 92 days (Table 4.6). Days to heading of20% of the F_3 populations were statistically shorter that the overall mean. The earliest populations with 70 days to heading were CT16323-CA-25-M x Vandana and NERICA 1 x Vandana. They had statistically significant shorter days to heading than their uncommon parents. The early class was dominated by crosses between E x E (eight populations) and E x EM (six populations). The common parents were NERICA 2 appearing in six crosses and Vandana and CT16323-CA-25-M appearing in five crosses each. In addition, 59% of the selected early maturing class were between interspecific and *Oryza sativa* lines. The latest maturing crosses with days to heading of 90 and 91 days were between *Oryza sativa* lines. These were Luyin 46 x IR55423-01 (M x M), Luyin 46 x IR55423-01 (M x M) and IR55423-01 x I R74371-54-1-1 (M x EM) in that rank order. The common parents in the late class were IR55423-01 and Luyin 46. Number of productive tillers per plant ranged from 6 to 12 with a mean of eight tillers per plant. The late maturing population NERICA-L-25 x IR74371-54-1-1 showed the highest number of productive tillers per plant of 12 tillers. The average plant height across environments was 100 cm ranging from 92 to 109 cm. Among the selected populations, *Duorado* x Vandana and CT16323-CA-25-M x Vandana were the tallest. The population CT16323-CA-25-M x Vandana combined shorter days to heading with higher number of productive tillers per plant of 10 tillers and tall plants of 108 cm.

Table 4.4: Mean values of the earliest maturing 9 and latest maturing 11 F_3 populations and their parents across no drought (Matuga, Mtwapa and Msabweni long rain season) environments

Genotypes	**DH†**	**DA**	**DM**	**TNO**	**PH**
F_3 populations with days to heading of 74 days and below					
CT16323-CA-25-M x Vandana (E x E‡)	70	72	96	9	105
NERICA 1 x Vandana (E x E)	71	73	98	8	102
NERICA 1 x CT16323-CA-25-M (E x E)	72	74	99	7	96
NERICA 1 x CT16333(1)-CA-22-M (E x EM)	73	76	103	8	102
NERICA 2 x CT16323-CA-25-M (E x E)	73	77	105	7	97
NERICA 2 x Luyin 46 (E x M)	73	76	109	9	101
NERICA 1 x *Dourado* (E x E)	74	79	102	7	98
CT16333(1)-CA-22-M x CT16323-CA-25-M (EM x E)	74	76	104	7	95
NERICA 2 x *Dourado* (E x E)	74	77	106	8	100
F_3 populations with days to heading of more than 80 days					
Duorado x CT16333(1)-CA-22-M (E x EM)	80	83	109	9	105
Duorado x NERICA-L-25 (E x M	80	84	108	9	97
CT16333(1)-CA-22-M x NERICA-L-25 (EM x M)	80	83	113	7	107
IR55423-01 x Vandana (M x E)	82	86	111	10	101
NERICA-L-25 x IR74371-54-1-1 (M x EM)	82	83	114	12	98
NERICA-L-25 x IR55423-01 (M x M)	84	87	115	10	103
Luyin 46 x NERICA -L- 25 (M x M)	84	88	117	11	99
CT16333(1)-CA-22-M x IR55423-01 (EM x M)	89	92	120	8	97
IR55423-01 x IR74371-54-1-1 M x EM)	91	94	121	9	103
Luyin 46 x IR55423-01(M x M)	91	95	123	11	100
Luyin 46 x IR74371-54-1-1 (M x EM)	92	96	109	11	89
Parents					
CT16323-CA-25-M	73	76	97	7	95
Vandana	73	74	98	10	96
NERICA 1	74	76	102	7	95
Duorado	74	77	99	8	108
NERICA 2	77	80	107	7	93
IR74371-54-1-1	82	84	109	10	93
CT16333(1)-CA-22-M	82	84	105	7	105
IR55423-01	88	91	117	11	95
NERICA -L- 25	92	94	118	12	103
Luyin 46	92	95	116	11	97
Mean Across	**78**	**81**	**108**	**9**	**99**
Min	**92**	**96**	**123**	**12**	**107**
Max	**70**	**72**	**96**	**7**	**89**
LSD $_{(0.05)}$	**3**	**3**	**2**	**2**	**8**
Matuga Mean	**79**	**83**	**110**	**9**	**93**
Mtwapa mean	**83**	**85**	**112**	**7**	**96**
Msambweni long rain mean	**72**	**75**	**101**	**101**	**108**

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height

‡E, Early maturing; EM, Early to medium maturing; M, Medium maturing; LSD, least square difference

Table 4.5: Mean values of the earliest maturing 15 and latest maturing 5 F_3 populations and their parents under random managed drought stress

Genotypes	DH†	DA	DM	TNO	PH
F_3 populations with days to heading of 71 days and below					
Duorado x IR74371-54-1-1 (E‡ XEM)	66	68	102	9	100
CT16323-CA-25-M x IR55423-01(E x M)	67	71	102	10	106
CT16323-CA-25-M x IR74371-54-1-1(E x EM)	67	69	99	9	99
NERICA 1 x Vandana (E x E)	69	71	96	8	101
CT16323-CA-25-M x Vandana (E x E)	70	72	96	10	118
NERICA 1x NERICA 2(E x E)	70	73	103	9	98
NERICA 2 x CT16333(1)-CA-22-M (E x EM)	70	74	104	7	97
NERICA 2 x Vandana (E x E)	70	73	109	8	98
Duorado x Vandana (E x E)	70	72	98	9	120
NERICA 1 x IR74371-54-1-1(E x EM)	71	73	102	9	105
NERICA 2 x IR55423-01(E x M)	71	73	103	10	98
NERICA 2 x IR74371-54-1-1(E x EM)	71	73	100	10	101
Luyin 46 x Vandana (M x E)	71	74	107	10	107
NERICA 2 x Luyin 46(E x M)	71	74	103	9	99
Vandana x IR74371-54-1-1(E x EM)	71	73	105	11	108
F_3 populations with days to heading of more than 80 days					
Luyin 46 x IR74371-54-1-1 (M x EM)	81	84	113	12	105
NERICA-L-25 x IR55423-01 (M x M)	81	87	119	10	84
NERICA-L-25 x Vandana (M x E)	84	87	116	9	111
IR55423-01 x IR74371-54-1-1 (M x EM)	87	89	123	9	97
Luyin 46 x IR55423-01 (M x M)	88	92	121	10	99
Parents					
Duorado	71	73	98	8	119
Vandana	72	74	96	10	111
NERICA 1	75	78	99	7	94
CT16323-CA-25-M	77	80	102	8	95
NERICA 2	77	81	104	8	94
CT16333(1)-CA-22-M	80	83	113	5	103
IR74371-54-1-1	82	86	112	10	99
Luyin 46	87	92	116	10	106
IR55423-01	88	91	118	10	95
NERICA-L-25	91	96	123	12	82
Means	**75**	**77**	**106**	**9**	**102**
Max	**88**	**92**	**123**	**12**	**120**
Min	**66**	**68**	**96**	**7**	**84**
LSD (0.05)	**6**	**6**	**5**	**2**	**10**

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height

‡E, Early maturing; EM, Early to medium maturing; M, Medium maturing; LSD, Least square difference

Table 4.6: Mean values of the earliest maturing 17 and latest maturing 8 F_3 populations and their parents across non stress and random managed stress environments

Genotypes	**DH†**	**DA**	**DM**	**TNO**	**PH**
F_3 populations with days to heading of 74 days and below					
CT16323-CA-25-M x Vandana (E x E‡)	70	72	96	10	108
NERICA 1 x Vandana(E x E)	70	73	98	8	101
NERICA 1 x CT16323-CA-25-M (E x E)	72	74	98	7	94
NERICA 1 x CT16333(1)-CA-22-M (E x EM)	73	76	103	7	101
CT16323-CA-25-M x IR55423-01 (E x M)	73	76	107	8	98
NERICA 2 x CT16323-CA-25-M (E x E)	73	77	104	6	95
Duorado x IR74371-54-1-1(E x EM)	73	75	105	8	99
NERICA 1 x *Duorado* (E x E)	73	78	102	7	98
CT16333(1)-CA-22-M x CT16323-CA-25-M (EM x E)	73	76	103	7	95
NERICA 2 x Vandana (E x E)	74	76	106	8	98
NERICA 2 x IR74371-54-1-1(E x EM)	74	76	104	9	95
Duorado x Vandana (E x E)	74	76	103	9	108
CT16333(1)-CA-22-M x Luyin 46 (E M x E)	74	77	107	8	100
NERICA 2 x CT16333(1)-CA-22-M (E x EM)	74	77	107	7	99
Duorado x Luyin 46 (E x M)	74	76	104	9	101
NERICA 2 x *Duorado* (E x E)	74	77	105	7	99
NERICA 2 x IR55423-01 (E x M)	74	77	106	9	99
F_3 populations with days to heading of more than 80 days					
NERICA -L- 25 x IR74371-54-1-1 (M x EM)	80	82	114	12	102
IR55423-01 x Vandana	80	83	110	11	102
Luyin 46 x NERICA -L- 25 (M x M)	82	86	116	10	100
NERICA -L- 25 x IR55423-01 (M x M)	83	87	116	10	98
CT16333(1)-CA-22-M x IR55423-01 (EM x EM)	85	89	119	8	97
Luyin 46 x IR74371-54-1-1 (M x EM)	89	93	110	11	93
IR55423-01 x IR74371-54-1-1 (M x EM)	90	93	121	9	102
Luyin 46 x IR55423-01 (M x M)	91	94	122	11	100
Parents					
Vandana	73	74	97	10	100
Duorado	74	76	99	8	111
CT16323-CA-25-M	74	77	98	7	95
NERICA 1	74	76	101	7	94
NERICA 2	77	80	106	7	93
CT16333(1)-CA-22-M	81	84	107	7	105
IR74371-54-1-1	82	84	110	10	94
IR55423-01	88	91	117	11	95
Luyin 46	91	94	116	11	99
NERICA -L- 25	92	95	119	12	98
Means	**77**	**80**	**107**	**9**	**100**
Max	**91**	**94**	**122**	**12**	**109**
Min	**70**	**72**	**96**	**6**	**92**
LSD (0.05)	**3**	**3**	**2**	**1**	**7**

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height

‡E, Early maturing; EM, Early to medium maturing; M, Medium maturing; LSD, Least square difference

4.3.4 Comparative maturity of the F_3 populations across environments

For convenience of the study, comparative maturity of the genotypes was based on days to heading since it is a key determinant of physiological maturity of rice (Jiang *et al.*, 2007). Thus days to heading was classified into five classes (Figure 3.1) as follows: a) Extra early (≤ 70); b) Early (71 – 74); Early to Medium (75 – 80); Medium (81 – 85); and Late (> 85). The frequency distribution of the F_3 populations showed that 51% were early maturing while 36% belonged to the early to medium maturing class.

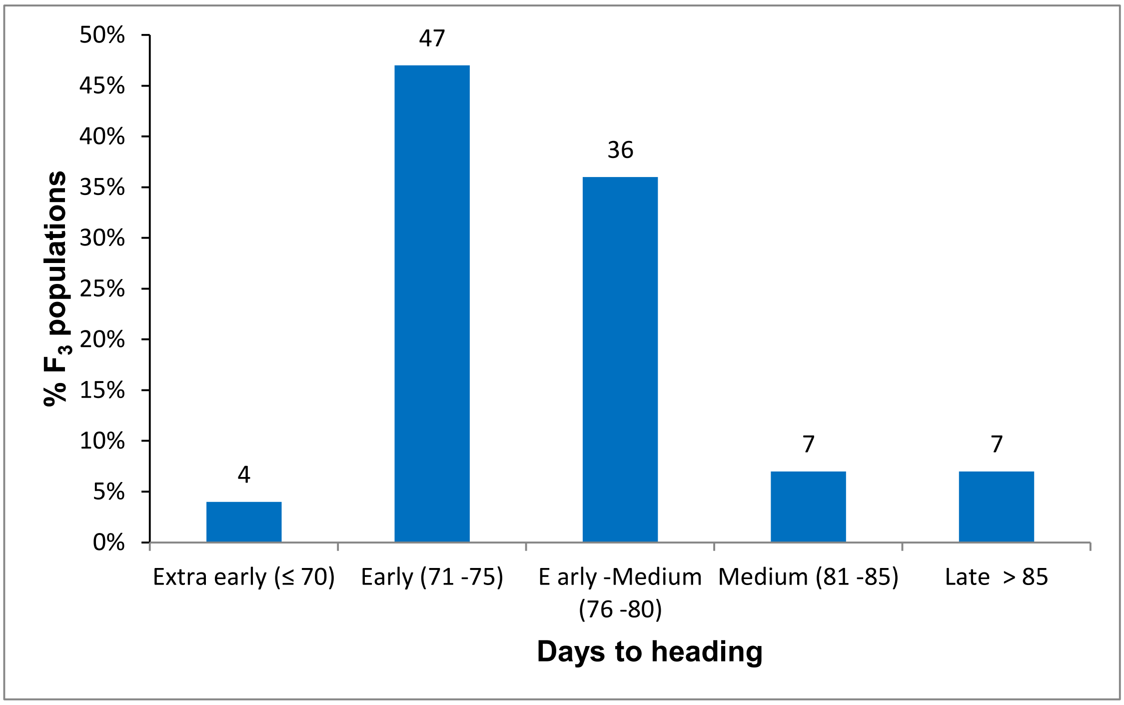

Figure 4.1 Frequency distribution of 45 crosses for days to heading across environment

4.3.5 Analysis of variance

Across no drought stress environments, mean squares due to genotype (G) and environment (E) main effects and their interactions were highly significant (p<0.01) for all traits measured with an exception of a non-significant mean squares due to G x E for number of productive tillers per plant (Table 4.7). Under random stress, means squares due to genotype main effects were highly significant (p<0.01) for all traits (Table 4.8). Across environments mean squares due to genotype and environment main effects were highly significant (p<0.01) for all traits. The G x E interaction was also highly significant (p<0.01) for all traits with an exception of a non-significant interaction effect for number of tillers per plant (Table 4.9).

4.3.6 Gene action

4.3.6.1 Across no drought stress environments

Across no drought stress environments, mean squares due to general combining ability (GCA) were highly significant ($p<0.001$) for all the traits (Table 4.7). The specific combining ability (SCA) mean squares were highly significant for phenological traits, significant ($p<0.05$) for number of productive tillers per plant and non-significant for plant height. The mean squares due to GCA and SCA and their interactions with the environment were highly significant for all traits with an exception of a significant SCA x E mean squares for number of productive tillers per plant. The GCA/SCA ratio was more than 0.5 for phenological traits and number of productive tillers per plant only.

4.3.6.2 Under random managed drought stress

Under random drought stress GCA and SCA mean squares were highly significant ($p<0.001$) for all traits with an exception of a significant ($p<0.05$) SCA for plant height and a non-significant SCA mean squares for number of productive tillers per plant (Table 4.8). The GCA/SCA ratio was more than 0.5 for days to maturity and number of productive tillers per plant only.

4.3.6.3 Across environments

Across no drought stress and random managed drought environments mean squares due to GCA and SCA and their interactions with the environment were highly significant ($p<0.01$) for all the traits measured except a significant ($p<0.05$) SCA for plant height and number of productive tillers per plant a non-significant SCA x E interaction effect for number of productive tillers per plant (Table 4.9). Although both GCA and SCA were significant, a larger contribution of the GCA effects (over 80%) to the total genetic sum of squares was observed for all the traits. This concurred with the GCA/SCA ratio which was more than 0.5 for all the traits measured.

Table 4.7: Analysis of variance and GCA/SCA ratio at each non stress environment for days to heading, days to anthesis, days to maturity, number of productive tillers per plant and plant height for the 45 F_3 progenies and their parents

Source of variation	**df**	**Mean squares**				
		DH† days	**DA days**	**DM days**	**TNO #**	**PH cm**
Environment (E)	2	3458.60***	2970.33***	3678.01***	389.41***	7071.41***
REP(E)	2	10.68	3.68	21.18**	0.33	27.56
Genotype (G)	54	196.78***	211.15***	205.77***	14.02***	100.86***
G x E	108	18.37***	20.23***	22.80***	2.39^{ns}	109.50***
GCA	9	705.88***	751.28***	904.10***	62.60***	219.90***
SCA	45	77.66***	84.64***	49.57***	3.27*	69.37ns
GCA*E	9	31.42***	34.19***	58.22***	13.05***	164.01***
SCA*E	45	37.67***	40.86***	44.10***	3.50*	226.16***
Error	162	5.98	6.27	3.82	2.14	47.94
CV		3.13	3.09	1.81	16.58	7.01
R^2		0.95	0.95	0.97	0.84	0.80
Mean		78.17	80.95	107.71	8.83	98.81
GCA/SCA ratio		0.58	0.57	0.74	0.78	0.27

*, **, ***, Significant at $p < 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†; DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height; GCA, General combining ability; SCA, Specific combining ability; CV, Coefficient of variation; R^2, Coefficient of determination

Table 4.8: Analysis of variance and GCA/SCA ratio under random managed drought stress at Msambweni for days to heading, days to anthesis, days to maturity, number of productive tillers per plant and plant height for the 45 F_3 progenies and their parents

Source of variation	**df**	**Mean squares**				
		DH† days	**DA Days**	**DM days**	**TNO #**	**PH cm**
Reps	1	5.68	8.74	13.83	1.06	77.95
Genotype (G)	54	66.03***	81.15***	111.19***	5.82***	137.42**
GCA	9	116.21***	159.15***	405.56***	23.54***	299.23***
SCA	45	50.96***	59.58***	44.19***	2.09ns	101.29*
Error	54	11.31	13.27	4.61	2.41	60.05
CV		4.51	4.70	2.03	17.80	7.61
GCA/SCA ratio		0.26	0.33	0.85	0.81	0.32

*, **, ***, Significant at $p < 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†; DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height; GCA, General combining ability; SCA, Specific combining ability; CV, Coefficient of variation; R^2, Coefficient of determination

Table 4.9: Analysis of variance and GCA/SCA ratio across environments (no drought and random managed drought stress) for days to heading, days to anthesis, days to maturity,, number of productive tillers per plant and plant height for the 45 F_3 progenies and their parents

Source of variation	df	Mean squares				
		DH† days	DA Days	DM days	TNO #	PH cm
Enviroment	3	2653.78***	2310.71***	2536.66***	259.93***	4972.49***
REP(E)	4	7.49	4.02	26.85**	1.44	111.13
Genotype (G)	54	236.89***	260.02***	289.41***	18.02***	137.31***
G x E	162	20.89***	24.25***	24.38***	2.20^{ns}	106.66***
GCA	9	772.57***	856.47***	1291.94***	83.97***	369.66***
SCA	45	106.46***	114.84***	63.75***	3.63*	81.15*
GCA*E	9	26.97***	29.38***	25.31***	5.07**	104.49**
SCA*E	45	19.94***	23.41***	24.70***	1.75^{ns}	105.22***
Error	216	7.31	8.02	4.01	2.21	50.97
CV		3.5	3.54	1.87	16.89	7.17
GCA/SCA ratio		0.79	0.79	0.97	0.97	0.59

*, **, ***, Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†; DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Number of productive tillers per plant; PH, Plant height; GCA, General combining ability; SCA, Specific combining ability; CV, Coefficient of variation; R^2, Coefficient of determination

4.3.7 General combining ability estimates

The general combining ability effects at each environment and across no drought conditions, under random managed drought stress and across environments are given in Table 4.10, for days to heading; Table 4.11, for days to anthesis; Table 4.12, for days to maturity; Table 4.13 number of tillers per plant and in Table 4.14, for plant height.

4.3.7.1 Across no drought stress

The GCA effects for days to heading and days to anthesis were consistently highly significant (p<0.001) and negative for the interspecific early maturing parents and positive for the medium maturing parents. The interspecific lines CT16323-CA-25-M (-3.53) and NERICA 1 (3.47) exhibited the lowest negative effects while the *Oryza sativa* lines IR55423-01 (4.53 days) and Luyin 46 (3.77) had the highest positive effects. The GCA effects for days to maturity were highly significant (p<0.001) to significant (p<0.05) for all the lines with an exception of CT16333(1)-CA-22-M. The effects were negative and lowest for NERICA 1 (-4.00) followed by Vandana (-3.95) and positive and highest for IR55423-01 (5.89), followed by NERICA-L-25 (4.72). For number of productive tillers per plant the interspecific lines with exception of NERICA-L-25 showed highly significant (p<0.001) negative effects with NERICA 1 showing the lowest effects of -1.14 tillers. On the other hand, the *Oryza sativa* lines with exception of *Duorado* precoce showed positive effects for number of productive tillers per plant with Vandana having the highest highly significant (P<0.001) effects followed by IR74371-54-1-1. The GCA effects for plant height were significant (P<0.05) and negative for line IR74371-54-1-1 only.

4.3.7.2 Under random managed drought stress

The GCA effects for days to heading were negative for all the early maturing lines with interspecific lines NERICA 2 (-1.95) and CT16323-CA-25-M (-1.85) showing the lowest highly significant (p<0.01) values. On the other hand, lines IR55423-01 (4.45) followed by NERICA-L-25 (3.15) had the highest highly significant (p<0.001) positive effects. For days to anthesis the *Oryza sativa* lines Vandana (-2.33) and *Duorado* precoce (-2.23) showed the lowest highly significant (p<0.01) and negative effects while IR55423-01 (5.43) followed by NERICA-L-25 (3.63) once more had the highest highly significant (p<0.001) positive effects. The GCA effects for days to maturity were highly significant (p<0.001) for all the lines with an exception of line CT16333(1)-CA-22-M. The lines CT16323-CA-25-M (-4.32) followed by NERICA 1 and *Duorado* precoce with -3.92 each, exhibited the lowest negative effects while IR55423-01 (7.14) followed by NERICA-L-25 (6.39) showed the highest positive effects for days to maturity. For number of productive tillers per plant the GCA effects were lowest, highly significant and negative for CT16333(1)-CA-22-M, *Duorado* precoce and NERICA 1 in that rank order. On the other hand, the effects were highest and positive for NERICA-L-25 followed by IR74371-54-1-1. The GCA effects for plant height were significant and negative for NERICA 2 followed by NERICA 1 and positive for Vandana followed by *Duorado precoce.*

4.3.7.3 Across environments

Across environments all the parents showed highly significant (p<0.01) GCA effects for phenological traits except for CT16333(1)-CA-22-M. The early maturing parents demonstrated negative GCA effects with interspecific lines CT16323-CA-25-M followed by NERICA 1 topping the list. On contrary, the medium maturing parents showed positive effects with *Oryza sativa* lines IR55423-01 followed by Luyin 46 topping the list. However, for days to maturity, parent NERICA-L-25 had the second highest positive GCA effect after IR55423-01. The GCA effects for number of productive tillers per plant were significant for all the parents. The effects were lowest and negative for NERICA 1 and highest and positive for IR74371-54-1-1. For plant height, GCA effects were significant and positive for *Duorado precoce* and Vandana only.

Table 4.10: The general combining ability effects (GCA) of parents for days to heading

Parents	**Days to heading**					
	MTG†	**MTP**	**MSM$_{LR}$**	**Across**	**MSM$_{SR}$**	**Across**
	No drought stress				**RMD**	
Interspecific						
NERICA 1	-3.92***	-4.14***	-2.35***	-3.47***	-0.75ns	-2.79***
NERICA 2	-2.07***	-4.39***	-2.10***	-2.85***	-1.95**	-2.63***
CT16323-CA-25-M	-3.57***	-4.44***	-2.60***	-3.53***	-1.85**	-3.11***
CT16333(1)-CA-22-M	-0.42ns	1.71**	0.06ns	0.45	-1.00ns	0.09ns
NERICA -L- 25	2.99***	3.76***	2.26***	3.00***	3.15***	3.04***
***Oryza sativa* L.**						
Vandana	-2.67***	-2.39***	-2.85***	-2.63***	-1.80*	-2.43***
Duorado precoce	-1.67**	-2.19***	-2.25***	-2.03**	-1.75*	-1.96***
IR74371-54-1-1	2.89***	2.86***	2.56***	2.77***	0.00ns	2.08***
Luyin 46	4.24***	4.16***	2.91***	3.77***	1.50*	3.20***
IR55423-01	4.19***	5.06***	4.36***	4.53***	4.45***	4.51***

*, **, ***, Significant at $p < 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain; RMD, Random managed drought stress

Table 4.11: The general combining ability effects (GCA) of parents for days to anthesis

Parents	**Days to anthesis**					
	MTG†	**MTP**	**MSM$_{LR}$**	**Across**	**MSM$_{SR}$**	**Across**
	No drought stress				**RMD**	
Interspecific						
NERICA 1	-3.61***	-4.18***	-2.53***	-3.44***	-0.98^{ns}	-2.82***
NERICA 2	-2.71***	-4.48***	-2.08***	-3.09***	-1.88*	-2.78***
CT16323-CA-25-M	-3.66***	-4.63***	-2.63***	-3.64***	-1.58*	-3.12***
CT16333(1)-CA-22-M	-0.61^{ns}	1.58**	-0.13^{ns}	0.28^{ns}	-1.23^{ns}	-0.10^{ns}
NERICA -L- 25	3.00***	3.88***	2.68***	3.18***	3.63***	3.29***
***Oryza sativa* L.**						
Vandana	-2.81***	-2.48***	-3.03***	-2.77***	-2.33**	-2.66***
Duorado precoce	-1.06^{ns}	-2.28***	-2.23***	-1.85**	-2.23**	-1.95***
IR74371-54-1-1	2.25***	2.88***	2.28***	2.47***	-0.53^{ns}	1.72**
Luyin 46	4.85***	4.13***	2.98***	3.98***	1.68*	3.41***
IR55423-01	4.35***	5.58***	4.68***	4.87***	5.43***	5.01***

*, **, ***, Significant at $p < 0.05$, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain; RMD, Random managed drought stress

Table 4.12: The general combining ability effects (GCA) of parents for days to maturity

Parents	Days to maturity					
	MTG†	MTP	MSM$_{LR}$	Across	MSM$_{SR}$	Across
	Non stress				RMS	
Interspecific						
NERICA 1	-4.37***	-3.13***	-4.51***	-4.00***	-3.92***	-3.98***
NERICA 2	-0.32ns	-2.98***	-1.36***	-1.55*	-2.07***	-1.68**
CT16323-CA-25-M	-3.62***	-4.03***	-3.41***	-3.68***	-4.32***	-3.84***
CT16333(1)-CA-22-M	0.94^{ns}	0.93*	0.10^{ns}	0.65^{ns}	-0.47^{ns}	0.37^{ns}
NERICA -L- 25	5.69***	2.83***	5.65***	4.72***	6.39***	5.14***
***Oryza sativa* L.**						
Vandana	-5.87***	-2.43***	-3.56***	-3.95***	-3.12***	-3.74***
Duorado	-2.47***	-2.18***	-3.01***	-2.55***	-3.92***	-2.89***
IR74371-54-1-1	0.09^{ns}	2.88***	1.95***	1.64*	2.14***	1.76**
Luyin 46	3.29***	3.13***	2.10***	2.84***	2.14***	2.66***
IR55423-01	6.64***	4.98***	6.05***	5.89***	7.14***	6.20***

*, **, ***, Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain; RMD, Random managed drought stress

Table 4.13: The general combining ability effects (GCA) of parents for number of productive tillers per plant

Parents	Tiller number					
	MTG†	MTP	MSM$_{LR}$	Across	MSM$_{SR}$	Across
	Well-watered				RMD	
Interspecific						
NERICA 1	-1.64***	-0.36^{ns}	-1.42***	-1.14***	-1.03**	-1.11***
NERICA 2	-1.62***	-0.40^{ns}	-0.75^{ns}	-0.92***	-0.60ns	-0.84***
CT16323-CA-25-M	-1.04***	-0.67**	-1.14**	-0.95***	-0.58ns	-0.86***
CT16333(1)-CA-22-M	-0.71**	-0.62*	-1.29**	-0.87***	-1.40***	-1.00***
NERICA -L- 25	0.94***	0.86***	1.09**	0.96***	1.29***	1.05***
***Oryza sativa* L.**						
Vandana	1.52***	0.42^{ns}	1.50***	1.15***	0.86**	1.08***
Duorado	-0.35^{ns}	-0.33^{ns}	-1.00*	-0.56*	-1.05**	-0.68**
IR74371-54-1-1	1.88***	0.35^{ns}	0.92^{ns}	1.05***	1.20***	1.09***
Luyin 46	0.59*	0.50*	1.66***	0.92***	0.63^{ns}	0.84***
IR55423-01	0.41*	0.27^{ns}	0.42ns	0.37	0.70*	0.45*

*, **, ***, Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain; RMD, Random managed drought stress

Table 4.14: The general combining ability effects (GCA) of parents for plant height

Parents	**Plant height**					
	MTG†	**MTP**	**MSM$_{LR}$**	**Across**	**MSM$_{SR}$**	**Across**
	No drought stress				**RMD**	
Interspecific						
NERICA 1	-0.84^{ns}	0.52^{ns}	-3.10^{ns}	-1.14	-3.79*	-1.80^{ns}
NERICA 2	-3.28**	0.55^{ns}	-0.59^{ns}	-1.11	-4.26**	-1.89^{ns}
CT16323-CA-25-M	-2.30*	-0.61^{ns}	-2.22^{ns}	-1.71	-2.18^{ns}	-1.83^{ns}
CT16333(1)-CA-22-M	4.12***	3.44***	-1.39^{ns}	2.06	0.29^{ns}	1.61^{ns}
NERICA -L- 25	0.64^{ns}	2.15*	1.23^{ns}	1.34	1.88^{ns}	1.47^{ns}
***Oryza sativa* L.**						
Vandana	3.72***	-1.03^{ns}	2.99^{ns}	1.89	6.88***	3.14**
Duorado	4.12***	0.87^{ns}	1.86^{ns}	2.28	4.29**	2.78**
IR74371-54-1-1	-3.12**	-3.50***	-1.40^{ns}	-2.67*	0.70^{ns}	-1.83^{ns}
Luyin 46	-2.43*	-1.97^{ns}	0.12^{ns}	-1.43	-0.06^{ns}	-1.08^{ns}
IR55423-01	-0.65^{ns}	-0.40^{ns}	2.51^{ns}	0.49	-3.75^{ns}	-0.57^{ns}

*, **, ***, Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively; ns, non-significant
†MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain; RMD, Random managed drought stress

4.3.8 Specific combining ability effects

4.3.8.1 Across no drought stress

Across well-watered environments SCA effects for days to heading were highly significant and negative for populations NERICA-L-25 x IR74371-54-1-1 followed by CT16333(1)-CA-22-M x Luyin 46 (Table 4.15). The other four populations showed significant ($p<0.05$) and negative SCA effects as well. Two populations CT16333(1)-CA-22-M x IR55423-01 and Luyin 46 x IR55423-01 had positive and significant SCA effects. For days to anthesis SCA effects were highly significant and negative for populations NERICA -L- 25 x IR74371-54-1-1, CT16333(1)-CA-22-M x Luyin 46, *Duorado* x IR55423-01 and NERICA 2 x Luyin 46 in that rank order. Six other crosses had significant and negative SCA effects. The effects were once more significant and positive for populations CT16333(1)-CA-22-M x IR55423-01 and Luyin 46 x IR55423-01. The SCA effects for days to maturity were significant and negative for populations NERICA 2 x IR55423-01 and *Duorado* x IR55423-01 only and positive for four populations with population Luyin 46 x IR55423-01 topping the list followed by IR55423-01xIR74371-54-1-1. For number of productive tillers per plant and plant height the effects were non-significant for all the populations with an exception of a significant and negative effect for population CT16333(1)-CA-22-MxNERICA -L- 25.

4.3.8.2 Under random managed drought stress

Nine F_3 populations showed significant SCA effects for days to heading (Table 4.16). Of these, the effects were lowest and negative for population CT16323-CA-25-M x IR74371-54-1-1, followed by population CT16323-CA-25-M x IR55423-01 while Luyin 46 x IR55423-01 showed the highest positive effects. The SCA effects for days to anthesis were significant for 10 populations and were lowest and negative for population NERICA-L-25 x IR74371-54-1-1 and highest and positive for Luyin 46 x IR55423-01. For days to maturity 15 populations showed significant effects with population CT16323-CA-25-M x IR74371-54-1-1 showing the lowest and negative effects while CT16323-CA-25-M x NERICA-L-25 showed highest and positive effects. All the F_3 populations showed non-significant SCA effects for number of productive tillers per plant. The F_3 population NERICA-L-25 x IR74371-54-1-1 showed the highest highly significant ($p<0.01$) and positive SCA effects for plant height.

4.3.8.3 Across environments

Specific combining ability (SCA) effects for all the characters under study across environments are presented in Table 4.16. The SCA effects for days to heading, days to anthesis and days to maturity were significant for less that 25% of the populations with a few populations showing positive effects. The populations NERICA-L-25 x IR74371-54-1-1 followed by CT16333(1)-CA-22-M x Luyin 46 showed the lowest highly significant negative SCA for days to heading and days to anthesis while population Luyin 46 x Vandana followed by NERICA 1 x NERICA 2 showed the highest significant ($P<0.01$) positive effects. For days to maturity population NERICA 2 x IR55423-01 showed the lowest negative SCA effect while population IR55423-01 x Vandana followed by Luyin 46 x NERICA-L-25 had the highest positive effects. All the F_3 populations showed non-significant SCA effects for number of productive tillers per plant while plant height was significant and positive for CT16323-CA-25-M x Vandana only.

Table 4.15: The specific combining ability effects (SCA) of F_3 populations for days to heading, days to anthesis, days to maturity, tiller number and plant height across no drought stress environments.

F_3 population	**DH†**	**DA**	**DM**	**TNO**	**PH**
NERICA 1 x NERICA 2	4.23	3.95	-0.94	0.76	1.7
NERICA 1 x *Duorado*	1.25	3.89	1.07	-0.03	-2.02
NERICA 1 x CT16333(1)-CA-22-M	-1.73	-1.58	-1.47	1.11	1.98
NERICA 1 x CT16323-CA-25-M	0.58	0.17	-1.14	-0.04	0.18
NERICA 1 x Luyin 46	-2.22	-3.28	-0.49	-1.06	1.62
NERICA 1 x NERICA -L- 25	0.55	0.35	1.13	-0.89	1.63
NERICA 1 x IR55423-01	-4.15	-3.83	-1.37	0.29	1.15
NERICA 1 x Vandana	-1.15	-1.37	-1.54	-0.47	1.9
NERICA 1 x IR74371-54-1-1	-3.07	-1.57	0.03	-0.57	-3.92
NERICA 2 x *Duorado*	1.3	1.04	1.95	0.28	-0.05
NERICA 2 x CT16333(1)-CA-22-M	-0.18	-0.27	0.92	-0.15	-0.18
NERICA 2 x CT16323-CA-25-M	1.63	2.49	1.92	-0.18	0.78
NERICA 2 x Luyin 46 (E x M)	**-5.67***	**-5.80****	-0.6	-0.22	5.06
NERICA 2 x NERICA -L- 25	-1.57	-1.33	-0.15	-0.37	-0.38
NERICA 2 x IR55423-01	-4.1	**-4.35***	**-4.65***	0.07	0.91
NERICA 2 x Vandana	2.4	2.29	2.52	-1.09	-1.51
NERICA 2 x IR74371-54-1-1 (E x EM)	**-8.28***	**-7.88***	-4.52	0.06	1.63
Duorado x CT16333(1)-CA-22-M	3.67	3.34	3.42	1.47	1.75
Duorado x CT16323-CA-25-M	3.32	3.25	**4.58***	0.19	1.44
Duorado x Luyin 46	-4.32	**-5.20***	-3.27	0.16	-0.23
Duorado x NERICA -L- 25	1.12	2.1	-1.99	0.2	-5.93
Duorado x IR55423-01 (E x M)	**-5.58***	**-6.08****	**-4.49***	-1.16	-1.19
Duorado x Vandana	1.75	1.39	3.52	-0.04	1.26
*Duorado*xIR74371-54-1-1	-3.47	-2.98	2.98	-1.12	-4.28
CT16333(1)-CA-22-M x CT16323-CA-25-M	-0.83	-1.22	-0.62	-0.02	-4.15
CT16333(1)-CA-22-M x Luyin 46 (EM X M)	**-6.30****	**-6.33****	-1.97	-1.04	-1.32
CT16333(1)-CA-22-M x NERICA -L- 25	-1.37	-1.2	-0.69	**-1.76***	4.55
CT16333(1)-CA-22-M x IR55423-01(EM x M)	**5.60***	**5.79****	**5.32***	0.17	-3.97
CT16333(1)-CA-22-M x Vandana	-0.07	0.42	0.65	-0.11	-1.29
CT16333(1)-CA-22-M x IR74371-54-1-1	-5.15	-5.02	3.02	-0.41	-2.09
CT16323-CA-25-M x Luyin 46	-0.32	-0.58	0.2	0.05	-5.87
CT16323-CA-25-M x NERICA-L- 25	-0.22	-0.78	1.82	0.08	-0.22
CT16323-CA-25-M x IR55423-01	-4.08	**-4.63***	-1.69	-0.42	-2.47
CT16323-CA-25-M x Vandana	-1.75	-2	-4.35	0.4	5.89
CT16323-CA-25-M x IR74371-54-1-1	-1.63	-2.1	5.85	0.42	5.89
Luyin 46 x NERICA -L- 25	-0.68	0.44	1.63	-0.01	0.49
Luyin 46 x IR55423-01 (M x M)	**5.12***	**5.09***	**6.30****	0.59	2.08
Luyin 46 x Vandana	0.28	1.05	-0.37	0.74	2.77
Luyin 46 x IR74371-54-1-1	1.00	2.02	-5.47	-0.74	-7.25
NERICA -L- 25 x IR55423-01	-1.95	-1.45	-3.09	-0.06	1.93
NERICA -L- 25 x Vandana	-1.95	-2.32	0.25	0.24	-4.36
NERICA -L- 25 x IR74371-54-1-1 (M x EM)	**-9.43****	**-10.28****	-0.75	-0.31	-1.24
IR55423-01 x Vandana	2.02	2.84	1.08	0.15	-0.32
IR55423-01 x IR74371-54-1-1	4.43	4.9	**8.08***	-2.03	10.91
Vandana x IR74371-54-1-1	-1.9	-0.57	2.42	1.78	8.98

*, **,*** indicates significant at 0.05, 0.01 and 0.001 probability levels, respectively

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, number of productive tillers per plant; PH, Plant height

Table 4.16: The specific combining ability effects (SCA) of F_3 populations for days to heading, days to anthesis, days to maturity, number of productive tillers per plant and plant height under random managed drought stress.

F_3 population	**DH†**	**DA**	**DM**	**TNO**	**PH**
NERICA 1 x NERICA 2 (E x E)	**5.10***	3.93	**3.22***	1.69	4.12
NERICA 1 x *Duorado*	0.90	0.78	2.07	0.68	-i5.87
NERICA 1 x CT16333(1)-CA-22-M	-0.85	-0.73	0.12	-0.37	-0.62
NERICA 1 x CT16323-CA-25-M	0.50	-0.88	-1.04	-0.23	-8.11
NERICA 1 x Luyin 46	-1.35	-1.63	-1.49	-1.79	-1.97
NERICA 1 x NERICA-L-25	-2.00	-2.58	-0.74	-0.80	-0.46
NERICA 1 x IR55423-01	1.20	4.63	2.52	0.93	**11.27***
NERICA 1 x Vandana	-3.05	-3.13	-3.24*	-0.82	-4.12
NERICA 1 x IR74371-54-1-1	-5.25	-5.45	-2.55	-0.73	6.46
NERICA 2 x *Duorado*	3.60	3.68	3.22*	-1.15	-5.16
NERICA 2 x CT16333(1)-CA-22-M	-1.15	-0.33	0.27	0.15	-0.86
NERICA 2 x CT16323-CA-25-M	2.70	4.03	2.12	-2.01	-6.94
NERICA 2 x Luyin 46	-2.65	-2.73	-2.84*	0.58	0.89
NERICA 2 x NERICA-L-25 (E x M)	**-6.30****	-7.18	-1.59	0.57	7.65
NERICA 2 x IR55423-01 (E x M)	**-6.10****	**-7.98****	**-8.34*****	0.85	4.18
NERICA 2 x Vandana	-0.35	0.28	**8.42*****	-1.15	-6.90
NERICA 2 x IR74371-54-1-1 (E x EM)	**-8.45***	**-9.35***	**-8.20*****	0.05	1.44
Duorado x CT16333(1)-CA-22-M	3.15	3.53	0.62	0.40	-1.80
Duorado x CT16323-CA-25-M (E X E)	**5.50***	**6.38****	**4.97*****	-0.67	3.26
Duorado x Luyin 46	-3.85	-4.38	-0.99	-1.08	-1.50
Duorado x NERICA-L-25	-3.50	-3.83	-5.74***	0.36	**10.01***
Duorado x IR55423-01	0.70	0.38	0.02	-1.35	-7.26
Duorado x Vandana	-0.55	-0.38	-1.24	0.64	6.40
Duorado x IR74371-54-1-1 (E x EM)	**-6.75***	-7.20	-2.05	-1.25	**-15.57***
CT16333(1)-CA-22-M x CT16323-CA-25-M	0.25	-0.13	-2.49	-0.02	-6.94
CT16333(1)-CA-22-M x Luyin 46 (EM x M)	**-6.60****	**-7.38****	**-6.94*****	1.22	3.05
CT16333(1)-CA-22-M x NERICA-L-25	-3.25	-3.83	**-8.19*****	0.61	**12.46***
CT16333(1)-CA-22-M x IR55423-01	-2.55	-2.13	**4.07****	-0.90	-2.96
CT16333(1)-CA-22-M x Vandana	2.70	2.63	-2.19	0.64	0.50
CT16333(1)-CA-22-M x IR74371-54-1-1	-6.50	-7.70*	-1.60	-0.75	-4.02
CT16323-CA-25-M x Luyin 46	-1.75	-2.53	-2.59	0.56	-2.94
CT16323-CA-25-M x NERICA-L-25	3.10	4.53	**9.17****	0.55	4.52
CT16323-CA-25-M x IR55423-01 (E x M)	**-10.20*****	**-9.78*****	**-7.09*****	0.73	**10.20***
CT16323-CA-25-M x Vandana	-0.95	-1.53	-2.84*	1.18	**11.32***
CT16323-CA-25-M x IR74371-54-1-1(E x EM)	**-11.35****	**-11.55****	**-9.95*****	-0.43	1.57
Luyin 46 x NERICA-L-25	-2.75	-3.23	-0.79	-0.91	-2.49
Luyin 46 x IR55423-01 (M x M)	**7.95*****	**7.98****	**5.97*****	0.07	0.84
Luyin 46 x Vandana	-3.30	-2.78	1.72	-0.13	-2.00
Luyin 46 x IR74371-54-1-1	-4.50	-5.80	-3.00	0.78	-1.17
NERICA-L-25 x IR55423-01	-0.70	0.53	-0.29	-1.19	**-16.20****
NERICA-L-25 x Vandana (M x E)	**8.55*****	**8.28*****	**6.47*****	-1.44	-0.24
NERICA-L-25 x IR74371-54-1-1 (M x EM)	**-14.35*****	**-15.35*****	**-7.25****	0.99	**32.63*****
IR55423-01 x Vandana	-2.75	-3.53	-2.79	1.89	1.44
IR55423-01 x IR74371-54-1-1	3.45	3.45	**10.00*****	-1.45	-2.26
Vandana x IR74371-54-1-1	-2.30	-2.30	3.75	0.81	2.78

*, **,*** indicates significant at 0.05, 0.01 and 0.001 probability levels, respectively

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, number of productive tillers per plant; PH, Plant height

Table 4.17: The specific combining ability effects (SCA) of F_3 populations for days to heading, days to anthesis, days to maturity, tiller number and plant height across environments

F_3 populations	**DH†**	**DA**	**DM**	**TNO**	**PH**
NERICA 1 x NERICA 2	**4.45***	**3.95***	0.10	1.00	2.31
NERICA 1 x *Duorado*	1.16	3.11	1.32	0.15	-2.98
NERICA 1 x CT16333(1)-CA-22-M	-1.51	-1.37	-1.07	0.74	1.33
NERICA 1 x CT16323-CA-25-M	0.56	-0.09	-1.11	-0.08	-1.89
NERICA 1 x Luyin 46	-2.00	-2.87	-0.74	-1.24	0.72
NERICA 1 x NERICA-L-25	-0.09	-0.38	0.67	-0.87	1.10
NERICA 1 x IR55423-01	-2.81	-1.72	-0.40	0.45	3.68
NERICA 1 x Vandana	-1.63	-1.81	-1.96	-0.56	0.40
NERICA 1 x IR74371-54-1-1	-3.61	-2.54	-0.61	-0.61	-1.33
NERICA 2 x *Duorado*	1.88	1.70	2.27	-0.07	-1.33
NERICA 2 x CT16333(1)-CA-22-M	-0.43	-0.28	0.75	-0.08	-0.35
NERICA 2 x CT16323-CA-25-M	1.90	2.87	1.97	-0.64	-1.15
NERICA 2 x Luyin 46 (E x M)	**-4.91****	**-5.03****	-1.16	-0.02	4.01
NERICA 2 x NERICA-L-25	-2.75	-2.79	-0.51	-0.14	1.63
NERICA 2 x IR55423-01 (E x M)	**-4.60***	-5.26	**-5.57****	0.26	1.73
NERICA 2 x Vandana	1.71	1.78	3.99	-1.11	-2.86
NERICA 2 x IR74371-54-1-1 (E x EM)	**-8.33****	**-8.25****	-5.44	0.06	1.59
Duorado x CT16333(1)-CA-22-M	3.54	3.38	2.72	1.20	0.86
Duorado x CT16323-CA-25-M	**3.86***	4.03*	**4.68****	-0.02	1.89
Duorado x Luyin 46 (E x M)	**-4.20***	**-4.99****	-2.7	-0.15	-0.55
Duorado x NERICA-L-25	-0.04	0.62	-2.92	0.24	-1.95
Duorado x IR55423-01 (E x M)	**-4.01***	**-4.47***	-3.36	-1.21	-2.71
Duorado x Vandana	1.18	0.95	2.33	0.13	2.55
Duorado x IR74371-54-1-1	-4.29	-4.04	1.73	-1.15	-7.10
CT16333(1)-CA-22-M x CT16323-CA-25-M	-0.56	-0.94	-1.09	-0.02	-4.85
CT16333(1)-CA-22-M x Luyin 46 (EM x M)	**-6.38*****	**-6.59*****	-3.21	-0.48	-0.23
CT16333(1)-CA-22-M x NERICA-L-25	-1.84	-1.86	-2.56	-1.17	6.52
CT16333(1)-CA-22-M x IR55423-01	3.56	**3.81***	**5.00****	-0.10	-3.72
CT16333(1)-CA-22-M x Vandana	0.63	0.97	-0.06	0.08	-0.84
CT16333(1)-CA-22-MxIR74371-54-1-1	-5.49	-5.69	1.86	-0.50	-2.57
CT16323-CA-25-M x Luyin 46	-0.68	-1.07	-0.5	0.18	-5.14
CT16323-CA-25-M x NERICA-L-25	0.61	0.55	**3.65***	0.19	0.97
CT16323-CA-25-M x IR55423-01 (E x M)	**-5.61****	**-5.92****	-3.04	-0.13	0.70
CT16323-CA-25-M x Vandana	-1.55	-1.88	**-3.97***	0.60	**7.25***
CT16323-CA-25-M x IR74371-54-1-1	-4.06	-4.46	2.88	0.21	4.81
Luyin 46 x NERICA-L-25	-1.2	-0.48	**6.22*****	-0.24	-0.25
Luyin 46 x IR55423-01 (M x M)	**5.83****	**5.81****	0.15	0.46	1.77
Luyin 46 x Vandana	-0.61	0.1	-4.85	0.52	1.58
Luyin 46 x IR74371-54-1-1	-0.38	0.06	1.8	-0.36	-5.73
NERICA-L-25 x IR55423-01	-1.64	-0.96	1.8	-0.34	-2.60
NERICA-L-25 x Vandana	0.68	0.33	-2.38	-0.18	-3.33
NERICA-L-25 x IR74371-54-1-1(Mx EM)	**-10.66*****	**-11.55*****	-2.57	0.02	7.23
IR55423-01 x Vandana	0.83	1.25	**8.56****	0.59	0.12
IR55423-01 x IR74371-54-1-1	4.19	4.54	-2.57	-1.89	7.62
Vandana x IR74371-54-1-1	-2	-1	-3.53	1.54	7.43

*, **,*** indicates significant at 0.05, 0.01 and 0.001 probability levels, respectively

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, number of productive tillers per plant; PH, Plant height

4.4 Discussion

4.4.1 Soil chemical properties

In all the study sites the soils were mainly sandy free draining with very low (< 0.1%) levels of organic matter. This contributed significantly to the low cation exchange capacity (CEC) observed in each site. As a result macro and micro nutrients were deficient in the soil. The soil chemical properties observed in this study are in agreement with findings from Mureithi *et al.* (1995) who observed that soils of the coastal region are mainly sandy with nitrogen as a major limiting element as it is easily leached during heavy rains. The water holding capacity and CEC are extremely low, resulting in poor efficiency of mineral fertilizers and low crop production. To correct low %N and P, inorganic N and P were applied. To correct the micro nutrients foliar feed was sprayed once during the tillering stage.

4.4.2 Performance of F_3 populations and their parents

The study revealed significant variability among genotypes and environment main effects and genotype x environment interaction for days to heading, days to anthesis, days to maturity, plant height and number of productive tillers per plant. The significant variations among the genotypes indicate presence of useful genetic variation among the parents and their respective progenies for the traits under study. Thus drought escaping varieties targeted for the coastal region in Kenya with high number of productive tillers per plant and desired plant height may be selected. However, since the environments varied, and there was a significant genotype x environment interaction, multi-location trials data would be necessary to identify best genotypes with specific or general adaptation. Heading date as characterised by the vegetative growth phase is a key determinant for physiological maturity of rice (Jiang et al., 2007). Various genetic manipulations of this phase have resulted in development of early maturing rice cultivars. Under random drought and across environments, over 50% of the early maturing populations with days to heading of less than 74 days were crosses between interspecific and *Oryza sativa* lines indicating the presence of unique allele combinations for earliness in these crosses which may be exploited to breed for early to extra early maturing varieties for the drought prone areas in sub-Saharan Africa. The populations CT16323-CA-25-M x Vandana (E x E) and NERICA 1 x Vandana (E x E) were found to be extra early and consistently showed shorter days to heading under no drought and random managed drought stress conditions. Parents of these populations including NERICA 2 appeared in most of the early maturing populations indicating that these parents may be good combiners for earliness. It also implies that the interspecific fixed lines used in this study were a potential source for earliness as revealed in other studies (Fukuta *et al.*, 2012). Under random managed drought stress a unique combination between *Oryza sativa* lines, was that of population Vandana x IR74371-54-1-1 (E x EM), combining earliness (71 days to heading) with medium number of productive tillers per plant of 11 tillers. Both of these parents have high reproductive stage drought tolerance (Venuprasad *et al.*, 2007, Verulkar *et al.*, 2010). Contrary to the green revolution in Asia where development of rice varieties was based on dwarfing genes, studies in sub-Saharan Africa have revealed that under rainfed conditions medium to tall varieties are preferred by farmers (Efisue et al., 2008). In this study populations combining short duration with increased plant height and higher number of productive tillers per plant such CT16323-CA-25-M x Vandana (E x E) and *Duorado* x Vandana (E x E) were identified. Selection of pure lines after homozygozity is reached from these crosses would mean availability of short duration cultivars with increased yield potential. This is because medium to tall plant height genes are associated with increased root depth and capacity to extract more soil moisture whereas higher number of productive tillers per plant would mean increased number of panicles per unit area. With the desired plant type, adoption of the new varieties is likely to be higher and faster.

4.4.3 Gene action

The study showed significant GCA and SCA mean squares for all traits with an exception of non-significant SCA mean squares for number of productive tillers per plant under random drought conditions and plant height under no drought conditions. The significant GCA and SCA mean squares indicated that both additive and non-additive gene action were important in expression of the traits involved. The non-significant SCA mean squares imply that non-additive gene action (dominance and epistasis effects) was less important in the expression of number of productive tillers per plant and plant height. However, further analysis on the ratio of additive to total genetic variance revealed that under random stress conditions, additive gene action seemed to be more important for days to maturity and number of productive tillers per plant, but non-additive genetic variance was more important for days to heading, days to anthesis and plant height. In contrast, additive gene action was more important for all the traits under no drought conditions and across environments. Other researchers have also reported the predominance of additive gene action in inheritance of earliness (Li and Chang, 1970; Abd Allah *et al.*, 2009), number of productive tillers per plant, (Efisue *et al.*, 2009) and plant height (Abd Allah *et al.,* 2009; Muthuramu *et al.*, 2010) and (Efisue *et al.*, 2009). The superiority of additive gene action in conditioning inheritance of earliness, number of tillers per plant and plant height under no drought conditions in materials under study indicates that direct selection using recurrent selection methods could be useful in isolating superior genotypes. For example, extra early materials flowering in less than 65 days to fit in the short rain season with higher number of productive tillers per plant and desired plant height may be selected. In contrast, under water stress conditions improvement for earliness and plant height could be very difficult because selection would be less effective in isolating and fixing superior genotypes due to predominance of dominance and epistasis effects.

4.4.4 Combining ability estimates

Estimation of GCA effects allows identification of superior parents that could be used to select better crosses for further breeding (Simmonds, 1989). The study showed that although all the early maturing lines showed desirable alleles for earliness, one interspecific line, CT16323-CA-25-M and one *Oryza sativa* line, Vandana, were the best general combiners for shorter days to heading, days to anthesis and days to maturity because they consistently showed significant and negative GCA effects under no drought, under drought and across environments. Thus these lines contribute desirable alleles for earliness to their progenies. The good combining ability for earliness in these lines was confirmed by their contribution to the extra early class (≤ 74 days) composed of populations NERICA 1 x Vandana and CT16323-CA-25-M x Vandana that demonstrated the shortest days to heading of 72 days contributing to shorter days to anthesis and maturity. Elsewhere, within and outside sub-Saharan Africa, these lines can be utilized as source material in breeding for drought escape in drought prone areas where drought is severe, predictable, and terminal. Further the line Vandana which has a high reproductive stage drought tolerance (Venuprasad *et al.*, 2007) showed significant positive GCA for number of productive tillers per plant and plant height across environments. This indicated that Vandana combined desirable alleles for earliness, higher number of productive tillers per plant and increased plant height. As stated earlier, selection of pure lines from crosses with Vandana would mean availability of short duration cultivars with increased yield potential. This is because medium to tall plant height genes are associated with increased root depth and capacity to extra more soil moisture whereas higher tiller number would mean increased number of panicles per unit area.

The SCA effects represent dominance and epistasis gene action. Expression of this type of gene action either reduces or enhances selection limits, but in general they distort predictions of genetic improvements (Kearsey and Pooni, 1996). In this study the top crosses having the lowest and desirable negative SCA for phenological traits were crosses between lines with desirable combining ability for earliness and lines with undesirable combining ability for lateness. Across environments these were NERICA 2 x IR74371-54-1-1, CT16323-CA-25-M x IR55423-01, NERICA 2 x Luyin 46, NERICA 2 x IR55423-01 and *Duorado* x Luyin 46 and *Duorado* x IR55423-01. In general these crosses were between interspecific x O*ryza sativa* lines. The early parents were mainly three interspecific lines; namely CT16323-CA-25-M, NERICA 2 and *Duorado* precoce while the late parents were mainly IR74371-54-1-1, IR55423-01 and Luyin 46. Earliness in these crosses was attributed to the interaction between negative alleles (alleles for earliness) from parents with desirable GCA for earliness and positive alleles (alleles for lateness) from parents with undesirable GCA for lateness. Earliness observed in these crosses was due to dominance and epistasis effects; selection would therefore be less effective in isolating and fixing superior genotypes in later generations (Sleper and Poehlman, 2006, Dwivedi and Pandey, 2012). For plant height there were more significant specific combiners under random drought stress than under no drought environments. The best specific combinations were crosses between tall x tall and short x tall plant height. The tall x tall combination observed from the crosses NERICA-L-25 x IR74371-54-1-1 and CT16333(1)-CA-22-M x NERICA-L-25 was due to additive x additive effects which is fixable in the later generations and therefore selection would be successful in isolating genotypes with increased plant height.

4.5 Conclusions

The objective of this study was to investigate a) inheritance of earliness; and b) combining ability for phenological and some morphological traits among interspecific and *Oryza sativa* pure lines and their crosses. In this study inheritance of earliness based on days to heading differed under drought and no drought condition. Under drought condition inheritance of earliness was found to be conditioned by non-additive gene action while under no drought conditions additive gene action prevailed. This was also observed for days to anthesis and plant height. For days to maturity and number of productive tillers per plant, additive gene action appeared to be more important under drought and no drought conditions. With predominance of additive gene action then improvement of these traits can be done under no drought conditions through recurrent selection strategy, which increases the frequency of favorable alleles with additive effects provided that the environment variations are held to the minimum. The study identified one interspecific line CT16323-CA-25-M and one *Oryza sativa* line, Vandana, as the best general combiners for shorter days to heading, days to anthesis and days to maturity under drought and no drought conditions. Thus these lines contributed alleles for earliness to their progenies. Of these lines Vandana had good GCA for increased tiller number and plant height. The best specific combinations that showed negative effects implying earliness were mostly crosses between interspecific x *Oryza* *sativa*. Earliness in these crosses was attributed to the interaction between negative alleles (alleles for earliness) from parents with desirable GCA for earliness and positive alleles (alleles for lateness) from parents with undesirable GCA for lateness. Since the observed earliness in these crosses was due to dominance and epistasis effects, selection would therefore be less effective in isolating and fixing superior genotypes in later generations. Based on average performance of the F_3 populations, the populations CT16323-CA-25-M x Vandana and *Duorado* x Vandana combined short duration with increased plant height and higher number of productive tillers per plant. Early generation testing in these crosses can be employed to identify plants with desirable characters thus reducing the breeding load. Selection of pure lines from crosses with *Duorado* and Vandana would mean availability of short duration cultivars with increased yield potential. This is because medium to tall plant height genes are associated with increased root depth and capacity to extra more soil moisture whereas higher tiller number would mean increased number of panicles per unit area.

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Chapter Five

Combining ability for grain yield and yield components in interspecific and *Oryza sativa* L. rice pure lines under drought and no drought conditions

Abstract

Drought tolerance in rice has been identified as a complex trait. However, knowledge of combining ability may contribute to understanding of the type of gene action involved in expression of grain yield and its contributing traits under water stress and non-stress conditions. The objective of this study was to determine combining ability and mode of gene action conditioning, grain yield and some yield contributing traits in rice. Five interspecific and five *Oryza sativa* L. lines were mated in half diallel mating design and the resulting F_1 progenies advanced to F_3 generation. The 45 F_3 populations, 10 parents and one check were evaluated in 7 x 8 alpha lattice design with two replications. The materials were evaluated under three no drought and one random managed drought stress condition at three sites in coastal lowlands of Kenya. A thousand grain weight, grains per panicle, panicle weight, weight of grains per panicle, grain phenotypic acceptability and grain yield were measured. Across environments, variation among genotypes was significant for all traits measured. The F_3 populations NERICA 1 x NERICA 2 and CT16323-CA-25-M x Vandana combined high yield potential (4 t ha^{-1}) with moderate drought tolerance index (1). Mean squares due to GCA and SCA were significant for grain yield and the other yield components. However, based on GCA/SCA predictability ratio, predominance of non-additive gene action was observed for grain yield, spikelet fertility, number of grains per panicle and weight of grains per panicle, while additive gene action was more important for a thousand grain weight under drought and no drought conditions. The O*ryza sativa* line Vandana exhibited good GCA effects for grain yield and percentage of spikelet fertility across no drought conditions (0.45 t ha^{-1}; 4.22%) and across environments (0.33 t ha^{-1}; 3.96%). The line *Duorado* precoce had the best GCA effect for a thousand grain weight. The interspecific line NERICA 2 was the best for grains per panicle while NERICA 1 had the best GCA effects for panicle weight, weight of grains per panicle and grain phenotypic acceptability. The rice pure lines with desirable traits could be used to improve grain yield and yield components in rainfed rice breeding programmes in sub-Saharan Africa.

Keywords: Drought, gene action, grain yield, general combining ability, rice, specific combining ability,

5.1 Introduction

Drought is a major constraint to rice production in the rainfed upland and lowland production ecosystems in sub-Saharan Africa (Efisue *et al.*, 2009). Drought stress greatly reduces rice production and productivity resulting in severe economic losses that directly affect the small-scale farmers (Jongdee *et al.*, 2006; Bhandari *et al.*, 2007; Ding *et al.*, 2007; Prapertchob *et al.*, 2007). In India, China and Thailand grain yield losses ranging from 9 to 64% under moderate stress (Ding *et al.*, 2007) and 100% under severe stress (Bhandari *et al.*, 2007) have been reported. In sub-Saharan Africa yield losses due to drought of up to 46% have been observed in Gambia (Diagne *et al.*, 2013). The effects of drought on rice production are likely to be aggravated by climate change particularly the warming temperature and unpredictability of rainfall (Wassmann *et al.*, 2009) threatening food security in the region; hence the need to breed for high yielding drought tolerant rice cultivars.

Although drought resistance in rice has been identified as a complex trait (Yue et al., 2005; Blum, 2011), knowledge of combining ability has contributed to understanding the type of gene action involved in expression of grain yield and its contributing traits under water stress and non-stress conditions (Jayasudha and Sharma, 2009; Lamo, 2009; Malarvizhi *et al.*, 2010). Some studies have concluded both additive and non-additive gene action as important (Kumar *et al.*, 2007a; 2007b). Others have revealed predominance of additive gene action over non-additive gene action (Lamo, 2009). Yet others have reported non-additive gene action was more important (Verma *et al.*, 2003; Verma and Srivastava, 2004; Kumar *et al.*, 2008b; Jayasudha and Sharma, 2009; Malarvizhi *et al.*, 2010). In a line x tester study of four cytoplasmic male sterile lines and 22 male parents evaluated under aerobic conditions, Malarvizhi *et al.* (2010) reported inheritance of grain yield per plant, spikelet fertility, 100-grain weight and number of grain per panicle was largely controlled by non-additive gene action. Under anaerobic conditions predominance of non-additive gene action for grain yield and spikelet fertility was also revealed (Jayasudha and Sharma, 2009). Further, among interspecific progenies, Lamo (2009) reported that additive effects were more important than non-additive effects for spikelet fertility and grains per panicle under water stress and non-stress environments. A major breakthrough on quantitative trait loci (QTL) analysis has been identification of a QTL located on chromosome 12 in Vandana/Way Rarem F_3-derived population, that has a large effect on grain yield under stress conditions accounting for 51% of the genetic variance (Bernier *et al.*, 2007). Selection and hybridization which utilize additive and non-additive gene action may be used to improve grain yield and its contributing traits under water stress and non-stress conditions.

Progress in breeding for cultivars adapted to the African environments has been achieved through development of interspecific fixed lines. These lines are known to carry better alleles for drought escape than the *O. sativa* L. cultivars (Jones *et al.*, 1997). Among the *O. sativa* L. cultivars the International Rice Research Institute (IRRI) rainfed upland and lowland breeding programme has also identified improved breeding lines for drought-prone environments (Verulkar *et al.*, 2010). A few of these materials have been introduced and some adopted in the coastal lowlands of Kenya. However, information on the genetic qualities of these materials including the local cultivars, which is useful in selection and development of new germplasm is lacking. To accelerate the development of high yielding adapted cultivars in the region, it is important to determine usefulness of these lines in combining ability studies. Therefore, the objective of this study was to determine a) combining ability; and b) the mode of gene action conditioning, grain yield and some contributing traits in crosses between interspecific and *Oryza sativa* L. rice pure lines.

5.2 Materials and methods

5.2.1 Germplasm, experimental sites, design and management

Description of the rice lines used in the 10 x 10 half diallel mating are presented in Chapter 4. Section 4.2.2 The experimental sites, experimental layout and management, have all been described in chapter 4 section 4.2.1 and 4.2.3 to 4.2.6.

5.2.2 Data collection

The Standard Evaluation System (SES) for rice reference manual (IRRI, 1996) was used for all traits measured except where stated. Thirty six plants were randomly selected and tagged for data collection. On each plant, data were collected on spikelet fertility (SF), one thousand grain weight (TGWT), number of grains per panicle (GPPN), weight of panicle (WTPN), weight of grains per panicle (WTGPPN), and grain phenotypic acceptability (GPACP). At physiological maturity a panicle from each of the tagged plants were harvested from each plot. Weight of panicle was measured at 14% moisture content using electronic balance. Thereafter, the total number of spikelets and unfilled spikelet was counted. Number of grains per panicle was obtained from the difference between the total number of spikelets and unfilled spikelets. After removing the unfilled spikelets, weight of grains per panicle was measured using electronic balance. Spikelet fertility was calculated as a percentage of total number of grains over total number of spikelets per panicle. One thousand seeds weight was obtained by individually counting 100 well developed whole grains. 36 samples were counted, dried to a moisture content of 14% and weighed using an electronic balance. The final weight was then converted to 1000 grain weight by multiplying by 10. Grain phenotypic acceptability was based on farmers' grain preference. Farmers in the region had indicated that they preferred long bold grains and big panicles. A score of 1 to 9 was used where 1, excellent; 3, good; 5, fair; 7, poor; 9, unacceptable. Grain yield was taken as the weight of unhulled grains harvested from an area of 2 m^2 for the experiments planted under field conditions and from 40 plants for the experiment planted in pots. This was then converted to tons ha^{-1} at 14% moisture content.

Drought stress tolerance for individual genotypes was determined by calculating relative drought index (RDI) based on theoretical aspects of selection under drought and no drought conditions (Fischedr and Maurer (1978) using the formula: RDI = Ys/Yns, where Ys = Yield under drought conditions and Yns = Yield under no drought conditions. In this study Msambweni long rain season represented the control condition (Yns). Relative drought indices greater than 1 indicate that the genotypes have relative tolerance to drought while relative drought indices smaller than one, indicates that the genotypes are sensitive to drought (Fischedr and Maurer, 1978).

5.2.3 Data analysis

Analyses of variance per environment and across environments were conducted using PROC GLM in SAS (SAS Institute, 2012), where parents were considered fixed effects and environments and replications and blocks within replications as random effects. General combining ability (GCA) effects of the parents and specific combining ability (SCA) effects of the crosses as well as their mean squares at each environment and across environments were estimated following Griffing's method 2 for the diallel formed by P parents and their P(P-1)/2 F1's, totaling n=P(P+1)/2 entries. Parents were considered as fixed effects (model 1) in the test of significance (Griffing, 1956). Diallel analysis was done using the DIALLEL-SAS program (Zhang *et al.*, 2005) according to the following linear model for individual environment: Xijk = μ + rk +gi + gj + sij + pij*k,* where Xijk = Observed measurement of the parent (i = j) or cross between ith and jth genotypes in the kth replicate; μ = the population mean; rk = the replication effect; gi = the GCA effect for the ith parent; gj = the GCA effect for the jth parent; sij = the SCA effect for the cross between ith and jth parent with sij = sji; pijk =experimental error. The interaction terms were used to test for the significance of the corresponding main effects. The environments and replications within environments were considered random effects and therefore tested against the residual error term.

The relative importance of GCA and SCA were estimated using the general predicted ratio (GPR) for the traits observed (Baker, 1978). The ratio was estimated as follows; $2\sigma^2$GCA/($2\sigma^2$GCA + σ^2SCA) where $2\sigma^2$GCA and σ^2SCA are the variance components for GCA and SCA, respectively, estimated from Griffing's method 2 model II (random effects). Ratios close to one indicate additive effects are important in the inheritance of the trait while ratios close to zero indicate dominance and epistasis effects are important in the inheritance of the trait.

5.3 Results

5.3.1 Mean performance of F_3 populations and their parents

In this study the check was found to be late maturing and was therefore eliminated from the analysis. Mean grain yield, yield components and relative drought index for the 45 F_3 populations and their parents across environments are presented in appendix A and B, whereas mean performance of the best fourteen and worst seven F_3 populations and the 10 diallel parents for grain yield per environment and across environments are presented in Table 5.1. The average grain yield for entries were 3.4 t ha^{-1} across no drought stress conditions, 3.0 t ha^{-1} under random managed drought, and 3.3 t ha^{-1} across environments. The relative yield reduction under random drought stress compared to no drought stress at Msambweni long rain season was 18%. Under random managed drought stress, the highest yielding F_3 populations was NERICA 1 x *Duorado* while the lowest was CT16333(1)-CA-22-M x IR55423-01. Across no drought stress, the highest yielding F_3 populations was NERICA-L-25 x Vandana while the lowest was CT16333(1)-CA-22-M x NERICA-L-25. Across environments, the highest yielding F_3 population was Luyin 46 x IR55423-01 though it was not statistically different from the populations which had grain yield of more than 4 t ha^{-1}. These were NERICA-L-25 x Vandana, Luyin 46 x Vandana, NERICA 1 x NERICA 2 and CT16323-CA-25-M x Vandana. Among the top 14 selected F_3 populations, six were crosses between interspecific x *Oryza sativa* lines, 6 others were crosses between *Oryza sativa* lines while only two were between the interspecific lines. The highest yielding parent was Vandana while the worst performer was NERICA-L-25.

The relative drought index ranged from 1.7 to 0.1 with a mean of 0.9 (Table 5.1) The F_3 populations were assigned to four classes according to their relative drought index values (Figure 5.1) as follows: tolerant (≥1.5); moderately tolerant (1.4 - 1.0); moderately susceptible (0.9 - 0.5); and highly susceptible (≤ 0.5). The frequency distribution of the F_3

Table 5.1: Mean performance of the best 14 and the worst 7 F_3 populations and 10 diallel parents for grain yield at each and across no drought stress, under random managed drought stress and across environments

Genotypes	**‡MTG**	**MTP**	**MSM_{LR}**	**Across**	**MSM_{SR}**	**Across**	**Relative Drought Index (RDI)**
		No drought stress			**RDS**		
The best 14 F_3 populations							
Luyin 46 x IR55423-01	4.35	3.00	6.46	4.60	4.32	4.53	0.68
NERICA-L-25 x Vandana	4.00	3.95	6.38	4.77	2.85	4.29	0.46
Luyin 46 x Vandana	4.78	2.29	6.91	4.66	2.92	4.23	0.43
NERICA 1 x NERICA 2	4.45	4.15	3.95	4.18	4.08	4.15	1.03
CT16323-CA-25-M x Vandana	4.44	3.36	4.20	4.00	4.04	4.01	1.00
NERICA-L-25 x IR55423-01	3.55	4.93	4.14	4.20	3.19	3.95	0.78
NERICA 2 x CT16333(1)-CA-22-M	3.66	3.40	4.16	3.74	4.45	3.91	1.14
Vandana x IR74371-54-1-1	5.12	3.98	3.68	4.26	2.88	3.91	0.91
NERICA-L-25 x IR74371-54-1-1	3.19	4.49	3.49	3.72	4.06	3.81	1.26
IR55423-01 x Vandana	3.27	4.32	3.81	3.80	3.78	3.79	0.99
Luyin 46 x IR74371-54-1-1	2.05	3.79	4.64	3.49	4.60	3.77	1.00
IR55423-01 x IR74371-54-1-1	3.09	4.09	3.39	3.52	3.91	3.62	1.16
NERICA 1 x Duorado	3.64	2.22	3.39	3.08	5.01	3.56	1.50
NERICA 2 x Duorado	5.38	2.63	3.32	3.77	2.70	3.50	0.84
The worst 7 F_3 populations							
Duorado x NERICA -L- 25	2.61	2.61	2.85	2.69	2.89	2.74	1.04
CT16323-CA-25-M x Luyin 46	2.68	2.21	3.40	2.76	2.53	2.70	0.75
Duorado x IR74371-54-1-1	2.39	3.27	2.37	2.68	2.19	2.55	0.95
CT16333(1)-CA-22-M x Luyin 46	2.71	2.25	2.82	2.59	2.33	2.53	0.91
NERICA 1 x Luyin 46	2.72	2.66	3.15	2.84	1.55	2.52	0.55
Duorado x IR55423-01	3.06	2.23	2.53	2.61	1.60	2.35	0.66
CT16333(1)-CA-22-M x IR55423-01	2.48	2.39	3.33	2.73	0.93	2.28	0.27
Parents							
Vandana	4.43	3.26	4.79	4.16	3.05	3.88	0.64
Duorado	3.80	3.36	3.72	3.63	4.23	3.78	1.13
Luyin 46	2.13	4.21	5.95	4.10	2.21	3.62	0.37
IR55423-01	4.61	3.73	3.73	4.02	2.36	3.61	0.65
NERICA 1	3.93	3.22	3.63	3.59	3.39	3.54	0.93
NERICA 2	3.63	3.28	3.63	3.51	3.47	3.50	0.96
IR74371-54-1-1	2.62	4.41	2.50	3.18	3.88	3.35	1.58
CT16333(1)-CA-22-M	3.95	3.14	3.11	3.40	2.61	3.20	0.89
CT16323-CA-25-M	3.78	3.45	2.24	3.16	3.32	3.20	1.49
NERICA -L- 25	2.68	3.51	5.11	3.77	0.63	2.98	0.12
Mean	**3.38**	**3.24**	**3.66**	**3.43**	**3.00**	**3.32**	**0.89**
Maximun	**5.38**	**4.93**	**6.91**	**4.77**	**5.01**	**4.53**	**0.12**
Minimum	**2.05**	**2.21**	**2.37**	**2.59**	**0.93**	**2.28**	**1.72**
$\text{LSD}_{(0.05)}$	**0.86**	**0.86**	**1.69**	**1.07**	**0.68**	**0.57**	**0.56**

‡MTG, Matuga; MTP, Mtwapa, MSM_{LR}, Msambweni long rain; MSM_{SR}, Msambweni short rain; RDS, Random drought stress; LSD, Least significance difference

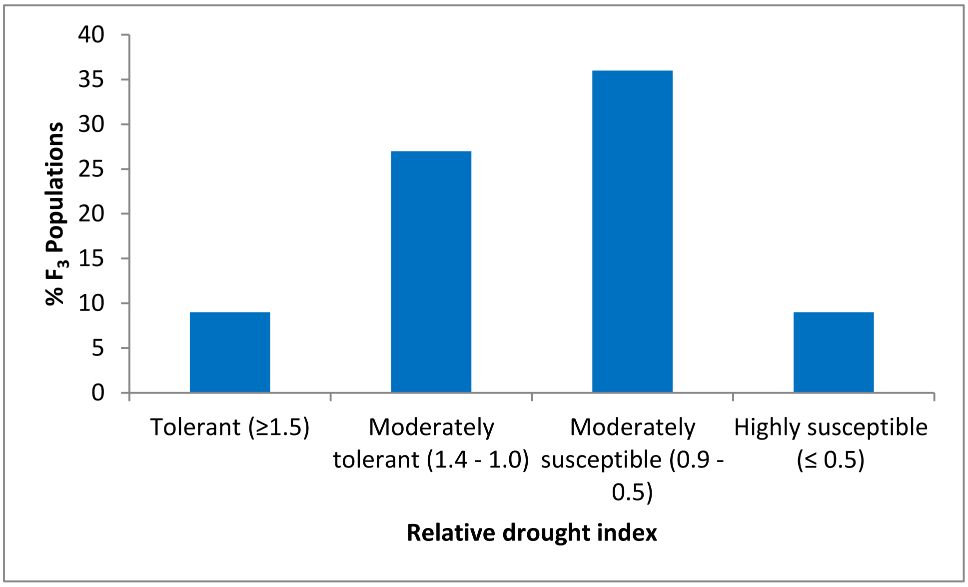

Figure 5.1: Frequency distribution of the 45 crosses for relative drought tolerance

populations showed that 9% were drought tolerant, while 27% were moderately drought tolerant. One population NERICA 1 x *Duorado* combined high yield potential with high drought tolerance index (1.5). The following populations combined high yield potential with moderate drought tolerance indices: NERICA 1 x NERICA 2 (1.0), CT16323-CA-25-M x Vandana (1.0), NERICA 2 x CT16333(1)-CA-22-M (1.1), NERICA-L-25 x IR74371-54-1-1 (1.26), Luyin 46 x IR74371-54-1-1 (1.0) and IR55423-01 x IR74371-54-1-1 (1.2). Among the parents, IR74371-54-1-1 had the highest index of 1.6 followed by CT16323-CA-25-M (1.5) and *Duorado* (1.1). Parents Vandana and IR55423-01 with known high and moderate reproductive stage drought tolerance, respectively, were found to be drought susceptible in this study.

The mean performance of the best fourteen and worst seven F_3 populations and the 10 diallel parents for grain yield components per environment and across environments are presented in Table 5.2. Spikelet fertility was highest for IR55423-01 x Vandana (88%), a thousand grain weight for NERICA 1 x *Duorado* (33 g), grains per panicle for IR55423-01 x I R74371-54-1-1 (139 grains), panicle weight and weight of grains per panicle for NERICA 1 x NERICA 2 (3.9 g and 3.47 g). The populations NERICA 1 x NERICA 2 and NERICA 1 x *Duorado* had the best grain phenotypic acceptability score of 1.8. Outstanding F_3 populations were NERICA 1 x NERICA 2 and NERICA 1 X *Duorado* and NERICA 2 x *Duorado* which combined higher yields with a higher a thousand grain weight of over 30 g, heavy panicle weight of over 3.5 g, heavy grains per panicle of over 3.0 g and a good grain phenotypic acceptability score of 2.

Table 5.2: Mean performance of the best 14 and the worst 7 F_3 populations and 10 diallel parents for yield components at across environments

Genotypes	**†SF**	**TGWT**	**GPPN**	**PNWT**	**WT-GPPN**	**GPACP**
The best 14 F_3 populations						
Luyin 46 x IR55423-01	85.24	23.33	130.69	3.14	2.64	5.13
NERICA-L-25 x Vandana	80.00	22.93	108.65	2.86	2.49	6.75
Luyin 46 x Vandana	86.96	24.51	119.68	2.91	2.58	5.88
NERICA 1 x NERICA 2	84.84	30.16	124.24	3.90	3.47	1.75
CT16323-CA-25-M x Vandana	85.24	28.01	115.26	3.35	2.99	4.63
NERICA -L- 25 x IR55423-01	83.67	23.31	120.10	3.09	2.64	5.25
NERICA 2 x CT16333(1)-CA-22-M	86.12	30.55	119.84	3.72	2.89	3.75
Vandana x IR74371-54-1-1	86.31	23.96	114.03	2.78	2.35	4.75
NERICA-L-25 x IR74371-54-1-1	78.18	22.82	107.56	2.76	2.30	5.13
IR55423-01 x Vandana	87.85	23.94	132.55	3.10	2.77	4.63
Luyin 46 x IR74371-54-1-1	85.44	24.02	121.14	2.94	2.61	4.63
IR55423-01 x IR74371-54-1-1	82.77	23.20	139.24	3.44	2.99	5.38
NERICA 1 x *Duorado*	83.99	31.18	105.48	3.63	3.08	1.75
NERICA 2 x *Duorado*	75.46	33.45	108.45	3.78	3.15	2.00
The worst 7 F_3 populations						
Duorado x NERICA -L- 25	59.86	26.15	99.13	2.53	1.93	5.75
CT16323-CA-25-M x Luyin 46	69.70	25.46	106.49	2.98	2.46	4.38
Duorado x IR74371-54-1-1	71.28	26.54	94.65	2.42	1.96	6.25
CT16333(1)-CA-22-M x Luyin 46	68.60	26.52	97.21	2.59	2.09	5.88
NERICA 1 x Luyin 46	69.02	27.17	108.85	3.34	2.90	4.25
Duorado x IR55423-01	67.39	28.73	87.08	2.68	2.22	6.00
CT16333(1)-CA-22-M x IR55423-01	62.76	27.67	96.00	2.68	2.10	4.88
Parents						
Vandana	88.19	23.54	111.46	2.70	2.48	7.88
Duorado	91.88	35.74	117.30	4.04	3.71	1.00
Luyin 46	80.67	23.03	122.13	2.79	2.51	4.88
IR55423-01	84.18	23.43	125.83	3.07	2.78	5.00
NERICA 1	85.70	29.65	125.29	4.16	3.75	1.00
NERICA 2	88.03	28.64	124.54	3.71	3.30	1.75
IR74371-54-1-1	89.46	22.86	131.81	3.18	2.82	4.50
CT16333(1)-CA-22-M	89.85	31.04	130.80	4.27	3.83	1.75
CT16323-CA-25-M	85.85	33.25	117.50	4.11	3.70	2.13
NERICA -L- 25	71.02	21.12	99.38	2.28	1.88	4.75
Entry mean Across	**78.81**	**27.01**	**112.68**	**3.14**	**2.69**	**4.33**
Maximun	**87.85**	**33.45**	**139.24**	**3.90**	**3.47**	**6.75**
Minimum	**59.86**	**22.82**	**87.08**	**2.42**	**1.93**	**1.75**
LSD$_{(0.05)}$	**6.76**	**1.82**	**14.40**	**0.44**	**0.41**	**0.85**
Matuga Mean	**75.97**	**25.40**	**104.12**	**2.87**	**2.50**	**4.36**
Mtwapa mean	**81.92**	**28.33**	**107.26**	**3.08**	**2.77**	**3.78**
Msambweni$_{LR}$ No drought stress	**83.57**	**27.83**	**136.63**	**3.75**	**3.15**	**4.31**
Msambweni$_{SR}$ Random managed stress	**73.77**	**26.47**	**102.69**	**2.87**	**2.35**	**4.87**

† SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability; LSD, Least significant difference

5.3.2 Analysis of variance

Across no drought stress environments, mean squares due to genotype and environment main effects and their interactions were highly significant (P<0.01) for grain yield and all the other yield contributing traits (Table 5.3). Under random drought stress, mean squares due to genotype main effects were also highly significant (P<0.01) for all traits (Table 5.4). Across environments mean squares due to genotype (G) and environment (E) main effects and their interactions were highly significant (P<0.01) for all traits (Table 5.5).

5.3.3 Gene action

5.3.3.1 Across no drought stress environments

Across no drought stress environments, mean squares due to general combining ability (GCA) and specific combining ability (SCA) were highly significant (p<0.01) for all the traits (Table 5.3). The mean squares due to GCA and SCA and their interactions with the environment were highly significant (p<0.01) for all traits with an exception of a non-significant mean squares due to GCA x E for a thousand grain weight. The GCA contribution to the total genetic sum of squares varied with traits. A thousand grain weight recorded the highest contribution of 97% while spikelet fertility had the lowest contribution of 45%.

5.3.3.2 Under random managed drought stress

Under random drought stress mean squares due to GCA and SCA were highly significant (p<0.001) for all traits with an exception of non-significant GCA mean squares for grain yield, a significant (p<0.05) GCA mean squares for spikelet fertility and a significant (p<0.05) SCA mean squares for a thousand grain weight (Table 5.4). The GCA contribution to the total genetic sum of squares varied with traits and was 17% for grain yield, 40% for spikelet fertility and above 50% for all the other yield contributing traits.

5.3.3.3 Across environments

Across environments mean squares due to GCA and SCA and their interactions with the environment were highly significant (p<0.001) for all the traits measured except a significant (p<0.05) GCA x E interaction effect for a thousand grain weight (Table 5.5). The GCA contribution to the total genetic sum of squares varied with traits and was 56% for grain yield and above 60% for all the yield components with an exception of spikelet fertility.

Table 5.3: Mean squares for grain yield, and yield contributing traits, and grain phenotypic acceptability of 45 F_3 populations and their parents across no drought stress conditions

Source of variation	**df**	**Mean squares**						
		†GY	**SF**	**TGWT**	**GPPN**	**PNWT**	**WTGPPN**	**GPACP**
Environment (E)	2	5.21***	1761.29***	269.35***	35358.84***	23.35***	11.73***	11.36***
REP(E)	3	0.72	30.67	0.25	98.49	0.08	0.03	0.42
Genotype (G)	54	1.79***	322.10***	65.74***	782.12***	1.20***	1.20***	15.66***
G x E	108	1.47***	126.24***	7.44***	563.53***	0.53***	0.54***	1.16***
GCA	9	3.43***	276.13***	302.51***	1416.69***	2.66***	2.11***	53.08***
SCA	45	1.50***	342.59***	10.46***	694.68***	0.84***	0.95***	6.35***
GCA*E	9	4.67***	329.10***	5.62	1344.94***	1.17***	1.35***	1.77***
SCA*E	45	0.79***	87.06***	7.81***	400.12**	0.38***	0.36***	1.09***
Error	162	0.36	37.02	4.10	229.11	0.18	0.15	0.57
CV		17.47	7.56	7.45	13.05	13.20	14.01	18.13
R^2		0.82	0.85	0.88	0.82	0.85	0.85	0.92
Mean		3.43	80.49	27.19	116.00	3.23	2.81	4.15
GCA/SCA ratio		0.01	0.06	0.98	0.23	0.37	0.25	0.83

*, **, *** Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability; GCA, General combining ability; SCA, specific combing ability; CV, Coefficient of variation; R^2 , Coefficient of determination

Table 5.4: Mean squares for grain yield, and yield contributing traits, and grain phenotypic acceptability of 45 F_3 populations and their parents under random drought stress

Source of variation	**df**	**Mean squares**						
		†GY	**SF**	**TGWT**	**GPPN**	**PNWT**	**WTGPPN**	**GPACP**
Reps	1	0.03	41.15	0.5	154.39	0.37	0.34	0.04
Genotype (G)	54	1.71***	273.03***	29.53***	825.61***	0.95***	0.93***	4.97***
GCA	9	0.40^{ns}	180.87*	148.56***	842.57***	2.48***	2.21***	10.90***
SCA	45	1.92***	270.57***	2.50*	742.47***	0.52***	0.56***	3.39***
Error	54	0.29	76.88	1.39	166.25	0.24	0.24	1.3
CV		17.82	11.89	4.46	12.56	16.98	20.88	23.36
R^2		0.86	0.78	0.96	0.83	0.8	0.8	0.79
Mean		3	73.77	26.47	102.69	2.87	2.35	4.87
GCA/SCA ratio		0.02	0.04	0.99	0.09	0.58	0.48	0.40

*, **, *** Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability; GCA, General combining ability; SCA, specific combing ability; CV, Coefficient of variation; R^2 , Coefficient of determination

Table 5.5: Mean squares for grain yield, and yield contributing traits, and grain grain phenotypic acceptability of 45 F_3 populations and their parents evaluated at across environments

Source of variation	df	Mean squares						
		†GY	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
Environment (E)	3	8.58***	2416.05***	193.87***	28446.70***	19.15***	13.56***	21.88***
REP(E)	4	0.54	33.29	0.31	112.47	0.16	0.11	0.33
Genotype (G)	54	2.08***	455.77***	91.62***	1016.32***	1.77***	1.80***	19.18***
G x E	162	1.46***	130.61***	6.18***	572.83***	0.48***	0.47***	1.25***
GCA	9	2.58***	366.02***	445.11***	1672.86***	4.54***	3.80***	60.94***
SCA	45	2.05***	472.50***	9.84***	911.16***	1.02***	1.22***	8.60***
GCA*E	9	3.53***	249.73***	5.73*	1092.09***	0.98***	1.07***	2.20***
SCA*E	45	0.99***	104.93***	6.25***	442.08***	0.36***	0.34***	1.11***
Error	216	0.34	46.98	3.43	213.39	0.2	0.18	0.75
CV		17.56	8.7	6.85	12.96	14.09	15.59	19.97
R^2		0.84	0.84	0.90	0.84	0.85	0.85	0.89
Mean		3.32	78.81	27.01	112.68	3.14	2.69	4.33
GCA/SCA ratio		0.11	0.05	0.99	0.20	0.56	0.39	0.78

*, **, *** Significant at $p< 0.05$, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability; GCA, General combining ability; SCA, specific combing ability; CV, Coefficient of variation; R^2 , Coefficient of determination

5.3.3.4 Relative importance of GCA and SCA effects

The relative importance of GCA and SCA variance was examined by expressing it as the ratio of additive to total genetic variance (Baker, 1978) (Table 5.6). For grain yield under no drought stress, the ratio was not consistent with additive variance accounting for 78% at Msambweni, 15% at Mtwapa and 1% across environments (Figure 5.1). Under random drought stress, additive genetic variance accounted for 2% of the total genetic variance. Across environments additive genetic variance accounted for 11% of the total genetic variance. For spikelet fertility (Figure 5.2), the ratio of additive to total genetic variance was consistently low accounting for between 29% at Matuga no drought stress to 5% across environments. The ratio of additive to total genetic variance for a thousand grain weight was consistently high recording 98% across no drought stress, and 99% at random drought stress and across environments (Figure 5.3). The relative importance of GCA and SCA effects for grains per panicle, panicle weight, weight of grains per panicle and grain phenotypic acceptability is given in Figure 5.4. For grains per panicle, additive genetic variance accounted for 23% across no drought stress, 9% under random drought stress and 20% across environments. Additive genetic variance for panicle weight and weight of grains per panicle accounted for 37% and 25% across no drought stress, 58% and 48% under random drought stress and 56% and 39% across environments, respectively. For grain phenotypic acceptability, additive genetic variance accounted for 83% across no drought stress, 40% under random stress and 78% across environment.

In general the results revealed that non-additive gene action was more important than additive gene action for grain yield, spikelet fertility, grains per panicle, and weight of grains per panicle under no drought and drought stress conditions. In contrast, additive gene action was more important for a thousand grain weight under no drought and drought stress condition. For panicle weight non additive gene action was more important under no drought stress while both additive and non-additive gene action prevailed under drought stress. For grain phenotypic acceptability, additive gene action was more important under no drought stress while non-additive gene action prevailed under drought stress conditions.

Table 5.6: Ratio of additive genetic variance to total genetic variance (based on Baker's ratio) for grain yield and yield contributing traits at each and across no drought stress, under random managed drought stress and across environments

Traits	**‡MTG**	**MTP**	**MSM$_{LR}$**	**Across**	**MSM$_{SR}$**	**Across**
		No drought condition			**RDS**	
Grain yield	0.23	0.15	0.78	0.01	0.02	0.11
Spikelet fertility	0.29	0.08	0.10	0.06	0.04	0.05
1000 grain weight	0.98	0.97	0.51	0.98	0.99	0.99
Grains per panicle	0.21	0.41	0.35	0.23	0.09	0.20
Panicle weight	0.53	0.33	0.21	0.37	0.58	0.56
Weight of grains per panicle	0.55	0.20	0.12	0.25	0.48	0.39
Grain phenotypic acceptability	0.59	0.93	0.73	0.83	0.40	0.78

‡MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain: RDS, Random managed drought stress

Bakers ratio: $2\sigma^2GCA/(2\sigma^2GCA + \sigma^2SCA)$

5.3.4 General combining ability effects

The estimates of GCA effects for grain yield varied significantly among lines and between environments (Table 5.7). Under each no drought stress environments, the lines showed inconsistency in the direction of the GCA estimates. Across no drought stress environments, Vandana displayed the highest significant and positive GCA effects (0.45 t ha^{-1}) while lines CT16323-CA-25-M, CT16333(1)-CA-22-M and *Duorado* showed significant negative effects. Under random drought stress the GCA effects were non-significant for all lines. Across environments, once more Vandana displayed the highest significantly positive GCA effects (0.33 t ha^{-1}). The GCA estimates for spikelet fertility were inconsistent in the sign under no drought stress environments for all lines with exception of Vandana which showed consistently positive GCA effects contributing to the highest highly significant positive GCA estimate of 4.22% across no drought stress environments (Table 5.8). Under random stress the estimates were significant ($p<0.01$) and negative for NERICA-L-25 only. Across environments Vandana showed the highest highly significant positive GCA estimate of 3.96%.

There was consistency in GCA estimates for a thousand grain weight (Table 5.9). The estimates were positive for all the interspecific lines with exception of NERICA-L-25 and negative for all the O*ryza sativa* lines with exception of *Duorado*. All the lines showed highly significant GCA estimates across no drought stress, under random drought stress and across environments. The line *Duorado* followed by CT16323-CA-25-M showed the highest positive effects at each and across environments while NERICA-L-25 had the lowest negative effects. The GCA effects for grains per panicle at and across environments were consistently positive for NERICA 2 and IR55423-01 and consistently negative for *Duorado* (Table 5.10). Across no drought stress the estimates were significant and positive for IR55423-01 and significant and negative for NERICA-L-25. Under random drought stress the estimates were significant and positive for NERICA 1 and NERICA 2 and significant and negative for NERICA-L-25 and *Duorado*. Across environments NERICA 2 displayed the highest positive estimate followed by IR55423-01 and NERICA 1 while *Duorado* showed the lowest negative estimates.

The GCA estimates for panicle weight and weight of grains per panicle were consistent at and across environments (Table 5.11 and 5.12). Once more, the estimates were positive for all the interspecific lines with exception of NERICA-L-25 and negative for all the O*ryza sativa* lines with exception of *Duorado*. Under random drought stress and across environments the lines NERICA 1 and NERICA 2 consistently showed the highest significant positive effects while NERICA-L-25 showed the lowest significant negative effects for panicle weight and weight of grains per panicle. The GCA estimates for grain phenotypic acceptability were consistently positive for all the interspecific lines with exception of NERICA-L-25 and negative for all the O*ryza sativa* lines with exception of *Duorado* (Table 5.13). Under random drought NERICA 1 followed by CT16323-CA-25-M showed the highest highly significant ($P<0.001$) negative estimates. Across no drought stress and across environments, NERICA 1 followed by NERICA 2 showed the highest highly significant ($P<0.001$) negative estimates. NERICA-L-25 followed by Vandana had the lowest significant GCA estimate.

Table 5.7 The general combining ability effects (GCA) of parents for grain yield (t ha^{-1})

Parents	Grain yield					
	MTG‡	**MTP**	**MSM_{LR}**	**Across**	**MSM_{SR}**	**Across**
	No drought stress				**RDS**	
Interspecific						
NERICA 1	0.22*	-0.15	-0.14	-0.03	0.18	0.03
NERICA 2	0.10	0.10	0.23	0.14	0.02	0.11
CT16323-CA-25-M	-0.03	-0.04	-0.71***	-0.26*	0.01	-0.19*
CT16333(1)-CA-22-M	0.14	-0.17	-0.63***	-0.22*	-0.21	-0.22*
NERICA-L-25	-0.44***	0.21*	0.45*	0.07	0.05	0.07
***Oryza sativa* L.**						
Vandana	0.58***	-0.09	0.86***	0.45**	-0.05	0.33***
Duorado	0.15	-0.30***	-0.76***	-0.30**	0.03	-0.22*
IR74371-54-1-1	-0.34***	0.45***	-0.3	-0.06	0.21	0.01
Luyin 46	-0.42***	-0.28**	1.05***	0.12	-0.16	0.05
IR55423-01	0.04	0.27**	-0.06	0.09	-0.08	0.04

‡MTG, Matuga; MTP, Mtwapa, MSM_{LR}, Msambweni long rain; MSM_{SR}, Msambweni short rain: RDS, Random managed drought stress

Table 5.8: The general combining ability effects (GCA) of parents for spikelet fertility (%)

Parents	Spikelet fertility					
	MTG‡	**MTP**	**MSM_{LR}**	**Across**	**MSM_{SR}**	**Across**
	No drought stress				**RDS**	
Interspecific						
NERICA 1	5.33***	-2.08*	-0.49	0.92	2.72	1.37
NERICA 2	2.72	-0.58	-1.33	0.27	1.47	0.57
CT16323-CA-25-M	2.92	2.10*	-2.38	0.88	2.11	1.19
CT16333(1)-CA-22-M	1.98	-1.2	-0.33	0.15	-2.37	-0.48
NERICA-L-25	-9.72***	2.21*	0.16	-2.45*	-4.99**	-3.09**
***Oryza sativa* L.**						
Vandana	5.39***	3.17**	4.09**	4.22***	3.18	3.96***
Duorado	2.11	-5.38***	-4.71***	-2.66*	-0.03	-2.00*
IR74371-54-1-1	-7.27***	1.7	2.05	-1.17	2.39	-0.28
Luyin 46	-5.62***	-0.33	1.85	-1.37	-3.42	-1.88
IR55423-01	2.16	0.38	1.09	1.21	-1.07	0.64

‡MTG, Matuga; MTP, Mtwapa, MSM_{LR}, Msambweni long rain; MSM_{SR}, Msambweni short rain: RDS, Random drought stress

Table 5.9: The general combining ability effects (GCA) of parents for a thousand grain weight (g)

Parents	A thousand grain weight					
	MTG‡	MTP	MSM$_{LR}$	Across	MSM$_{SR}$	Across
	No drought stress				RDS	
Interspecific						
NERICA 1	1.55***	1.11**	1.08	1.22***	1.99***	1.43***
NERICA 2	1.06**	1.31***	1.04	1.02***	1.80***	1.30***
CT16323-CA-25-M	2.42***	2.36***	2.13***	2.44***	2.54***	2.36***
CT16333(1)-CA-22-M	2.31***	1.82***	0.94	1.76***	1.63***	1.68***
NERICA-L-25	-3.88***	-3.51***	-2.28***	-3.17***	-3.71***	-3.35***
Oryza sativa **L.**						
Vandana	-1.22***	-1.68***	-0.91	-1.34***	-2.41***	-1.55***
Duorado	3.17***	3.57***	2.53***	3,23***	3.72***	3.25***
IR74371-54-1-1	-1.57***	-1.50***	-2.01***	-1.93***	-1.82***	-1.73***
Luyin 46	-2.00***	-1.32***	-1.53**	-1.70***	-1.60***	-1.61***
IR55423-01	-1.85***	-2.15***	-0.99	-1.69***	-2.14***	-1.78***

‡MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain: RDS, Random drought stress

Table 5.10: The general combining ability effects (GCA) of parents for grains per panicle (g)

Parents	Grains per panicle					
	MTG‡	MTP	MSMLR	Across	MSMSR	Across
	No drought stress				RDS	
Interspecific						
NERICA 1	6.89*	-0.91	-6.6	-0.21	9.96***	2.34*
NERICA 2	10.58**	2.53	3.12	5.41	6.38*	5.04**
CT16323-CA-25-M	-1.14	-4.88*	-1.82	-2.61	0.65	-1.76
CT16333(1)-CA-22-M	1.96	1.38	-13.10***	-3.25	1.87	-0.79
NERICA-L-25	-10.40**	9.19***	0.49	-0.24	-10.48***	-4.10*
Oryza sativa **L.**						
Vandana	3.61	-3.85	8.07*	2.61	-3.79	0.08
Duorado	-0.41	-17.00***	-12.30**	-9.90***	-7.93**	-8.12***
IR74371-54-1-1	-8.31*	11.03***	4.06	2.26	3.02	2.98
Luyin 46	-9.13**	-1.03	10.34**	0.06	-0.58	0.04
IR55423-01	6.36	3.52	7.74*	5.87*	0.91	4.30*

‡MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain: RDS, Random drought stress

Table 5.11: The general combining ability effects (GCA) of parents for panicle weight (g)

Parents	Panicle weight					
	MTG‡	MTP	MSMLR	Across	MSMSR	Across
	No drought stress				RDS	
Interspecific						
NERICA 1	0.42***	0.15*	0.24*	0.27**	0.58***	0.35***
NERICA 2	0.36***	0.23***	0.43***	0.34***	0.30**	0.33***
CT16323-CA-25-M	0.17	0.04	0.06	0.09	0.26*	0.14*
CT16333(1)-CA-22-M	0.34***	0.26***	-0.33**	0.09	0.13	0.10
NERICA-L-25	-0.60***	-0.08	-0.21	-0.30***	-0.45***	-0.34***
***Oryza sativa* L.**						
Vandana	-0.17	-0.25***	0.15	-0.09	-0.39***	-0.17*
Duorado	0.33***	-0.20**	-0.28**	-0.05	0.14	0.00
IR74371-54-1-1	-0.35***	0.01	-0.11	-0.15	-0.25*	-0.18*
Luyin 46	-0.39***	-0.09	-0.04	-0.17*	-0.13	-0.16
IR55423-01	-0.10	-0.07	0.09	-0.03	-0.20*	-0.07

‡MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain: RDS, Random drought stress

Table 5.12: The general combining ability effects (GCA) of parents for weight of grains per panicle (g)

Parents	Weight of grains per panicle					
	MTG‡	MTP	MSMLR	Across	MSMSR	Across
	No drought stress				RDS	
Interspecific						
NERICA 1	0.45***	0.08	0.24**	0.25***	0.53***	0.32***
NERICA 2	0.37***	0.25***	0.11	0.24***	0.29**	0.26***
CT16323-CA-25-M	0.21*	0.10	0.05	0.12	0.31**	0.17**
CT16333(1)-CA-22-M	0.32***	0.22**	-0.31***	0.08	0.02	0.06
NERICA-L-25	-0.66***	-0.10	-0.17*	-0.31***	-0.50***	-0.36***
***Oryza sativa* L.**						
Vandana	-0.12	-0.16*	0.22**	-0.02	-0.27**	-0.08
Duorado	0.35***	-0.21**	-0.26**	-0.04	0.11	0.00
IR74371-54-1-1	-0.37***	-0.01	-0.06	-0.15*	-0.21*	-0.16*
Luyin 46	-0.43***	-0.10	0.11	-0.14	-0.06	-0.12
IR55423-01	-0.13	-0.07	0.06	-0.04	-0.23*	-0.09

‡MTG, Matuga; MTP, Mtwapa, MSM$_{LR}$, Msambweni long rain; MSM$_{SR}$, Msambweni short rain: RDS, Random drought stress

Table 5.13: The general combining ability effects (GCA) of parents for grain phenotypic acceptability (g)

Parents	Grain phenotypic acceptability					
	MTG‡	**MTP**	**MSMLR**	**Across**	**MSMSR**	**Across**
		No drought stress			**RDS**	
Interspecific						
NERICA 1	-1.25***	-0.84***	-0.91***	-1.00***	-1.08***	-1.02***
NERICA 2	-0.95***	-1.04***	-0.86***	-0.95***	-0.58*	-0.86***
CT16323-CA-25-M	-0.65***	-0.84***	-0.81***	-0.77***	-0.88***	-0.79***
CT16333(1)-CA-22-M	-0.55**	-1.44***	-0.26	-0.75***	0.22	-0.51***
NERICA-L-25	1.35***	1.36***	0.80***	1.17***	0.72**	1.06***
***Oryza sativa* L.**						
Vandana	0.85***	1.36***	1.05***	1.09***	0.72**	0.99***
Duorado	-0.55**	-0.74***	-0.66***	-0.65***	-0.48*	-0.61***
IR74371-54-1-1	0.75***	0.56***	0.35*	0.55***	0.22	0.47***
Luyin 46	0.45**	0.76***	0.55**	0.59***	0.32	0.52***
IR55423-01	0.55**	0.86***	0.75***	0.72***	0.82***	0.74***

‡MTG, Matuga; MTP, Mtwapa, MSM_{LR}, Msambweni long rain; MSM_{SR}, Msambweni short rain: RDS, Random drought stress

5.3.5 Specific combining ability effects

The positive SCA effects were desirable for grain yield and all the other yield components while negative values were desirable for grain phenotypic acceptability. Under random drought stress, nine populations displayed significant ($p<0.05$) and positive estimates of SCA for grain yield (Table 5.14) The population NERICA-L-25 x IR74371-54-1-1 had the highest estimate of 3.3 t ha^{-1}. It also displayed the highest significant and positive estimates for spikelet fertility, grains per panicle, panicle weight and weight of grains per panicle. The second best was Luyin 46xIR74371-54-1-1 and in addition to positive estimates for grain yield it also showed the significant and positive estimates for panicle weight and weight of grains per panicle. The population NERICA 2 x CT16333(1)-CA-22-M had the highest significant and positive estimates for grains per panicle. However, it showed significant and positive estimates for grain phenotypic acceptability.

Across no drought conditions only three populations recorded significant ($p<0.05$) and positive SCA estimates for grain yield (Table 5.15). These were Luyin 46 x IR55423-01, NERICA-L-25 x Vandana and Luyin 46 x Vandana. Of these, Luyin 46 x IR55423-01 had significant ($p<0.05$) and positive SCA estimates for spikelet fertility and grains per panicle while Luyin 46 x Vandana showed significant (p<0.05) and positive SCA estimates for spikelet fertility.

Across environments, four populations displayed significant (p<0.05) and positive SCA estimates for grain yield and the best population was Luyin 46 x IR55423-01 (Table 5.16). It also showed significant and positive SCA estimates for spikelet fertility and grains per panicle. In addition to significant and positive SCA estimates for grain yield, the population NERICA 2 x CT16333(1)-CA-22-M had significant and positive estimates for spikelet fertility though it showed significant and positive estimates for grain phenotypic acceptability.

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Table 5.14: The specific combining ability of F_3 populations for grain yield and yield components under random stress condition.

F_3 populations	**GY†**	**SF**	**TGWT**	**GPPN**	**PNWT**	**WTGPPN**	**GPACP**
NERICA -L- 25 x IR74371-54-1-1	3.27***	27.88**	0.85	39.3*	1.31**	1.22*	0.50
Luyin 46 x IR74371-54-1-1	2.03***	1.37	2.01	22.65	1.24*	1.03*	-0.90
NERICA 1 x *Duorado*	1.79***	11.65*	-1.11	2.71	0.29	-0.06	-0.42
NERICA 2 x CT16333(1)-CA-22-M	1.63***	13.35*	-0.43	27.00**	0.05	-0.09	2.38**
Luyin 46 x IR55423-01	1.55***	12.25*	-0.70	17.43	0.43	0.29	-1.12
IR55423-01 x IR74371-54-1-1	1.26*	-10.04	-1.62	5.49	-0.32	-0.38	1.60
CT16333(1)-CA-22-M x NERICA -L- 25	1.10**	-2.90	-1.69*	20.76*	-0.45	-0.40	1.08
CT16323-CA-25-M x Vandana	1.08**	8.00	-0.19	14.48	0.50	0.44	-0.82
IR55423-01 x Vandana	0.90*	4.58	0.34	31.08	0.39	0.51	-1.52*
NERICA 1 x NERICA 2	0.87*	7.19	0.42	2.25	0.07	0.30	-0.32
Duorado x CT16323-CA-25-M	0.87*	7.09	1.53*	17.97*	0.23	0.39	-0.62
CT16323-CA-25-M x NERICA -L- 25	0.87*	6.10	0.03	-18.63*	-0.40	-0.47	1.18
NERICA 2 x NERICA -L- 25	0.78*	6.38	-1.46	13.7	0.06	-0.01	-0.12
Duorado x IR74371-54-1-1	-2.22***	-17.57*	-3.16**	-30.10*	-0.85	-1.02*	5.30***
CT16333(1)-CA-22-M x IR55423-01	-1.79***	-18.20**	2.84**	-27.38**	-0.63*	-0.65*	0.98
NERICA 2 x IR74371-54-1-1	-1.64**	-26.75**	0.89	9.76	-0.44	-0.59	1.2
NERICA 2 x CT16323-CA-25-M	-1.51***	-10.65	1.12	-10.84	-0.22	-0.03	-0.52
NERICA 1 x Luyin 46	-1.48***	-23.02***	0.22	-7.49	0.36	0.42	0.78
Duorado x IR55423-01	-1.36***	-26.52***	-1.86*	-34.69***	-0.79*	-0.74*	2.68***
NERICA 1 x NERICA -L- 25	-1.02**	-0.64	0.26	17.02*	0.22	0.21	0.38
Duorado x Luyin 46	-0.91**	-18.39**	-1.16	-23.05**	-0.77*	-0.79*	1.18
NERICA 1 x Vandana	-0.68*	-11.83*	0.19	-15.53	-0.07	-0.07	1.38

*, **, *** Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability

Table 5.15: The specific combining ability of F_3 populations for grain yield and yield components across no drought stress environments

F_3 populations	**GY†**	**SF**	**TGWT**	**GPPN**	**PNWT**	**WTGPPN**	**GPACP**
Luyin 46 x IR55423-01	0.99**	7.04*	-0.03	13.22	0.20	0.16	-0.37
NERICA -L- 25 x Vandana	0.84*	2.29	1.07	5.82	0.33	0.36	0.18
Luyin 46 x Vandana	0.68*	7.40*	0.67	5.81	0.22	0.21	-0.40
Duorado x IR74371-54-1-1	-1.19*	-23.91***	-2.42***	-35.98*	-1.64***	-1.78***	3.80***
CT16333(1)-CA-22-M x Luyin 46	-0.71*	-10.56**	-1.06	-11.47	-0.43	-0.49*	1.77***
Duorado x Vandana	-0.68*	-3.01	-2.83***	-6.75	-0.49	-0.48*	0.67
CT16333(1)-CA-22-M x NERICA -L- 25	-0.68*	-4.16	-1.77**	-11.5	-0.25	-0.21	0.85*
NERICA 2xVandana	-0.67*	-7.53*	1.21	0.92	0.05	-0.01	0.13

*, **, *** Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN**,** Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability

Table 5.16: The specific combining ability of F_3 populations for grain yield and yield components across environments

F_3 populations	GY	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
Luyin 46 x IR55423-01	1.13***	8.34**	-0.26	13.68**	0.26	0.19	-0.56
NERICA 1 x NERICA 2	0.71*	4.76	0.44	4.19	0.1	0.23	-0.79*
NERICA 2 x CT16333(1)-CA-22-M	0.71*	7.89*	0.59	2.92	0.17	-0.08	0.69*
NERICA -L- 25 x Vandana	0.59*	0.99	0.85	0	0.25	0.27	0.28
Duorado x IR74371-54-1-1	-1.45**	-22.32***	-4.22***	-12.89**	-1.45***	-1.59***	4.18***
NERICA 1 x Luyin 46	-0.86**	-8.61**	0.37	-6.21	0.04	0.04	0.33
CT16333(1)-CA-22-M x IR55423-01	-0.85**	-15.54***	0.8	-20.18***	-0.47*	-0.53**	0.22
Duorado x IR55423-01	-0.78**	-9.39**	0.29	-21.78***	-0.36	-0.34	1.44***
Duorado x Vandana	-0.65*	-0.22	-2.07**	-4.78	-0.37	-0.38	0.44
NERICA 2 x Vandana	-0.63*	-6.50*	0.82	0.31	0.01	-0.06	-0.18
CT16333(1)-CA-22-M x Luyin 46	-0.61*	-7.17*	-0.53	-14.71***	-0.47*	-0.51*	1.44***

*, **, *** Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN**,** Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, grain phenotypic acceptability

5.3.6 Correlation of GCA and SCA estimates and mean of grain yield and the yield components

There was no significant correlation between mean performance of the parents and their GCA effects for grain yield, spikelet fertility and grains per panicle (Table 5.17 below diagonal). However, a positive and highly significant ($p \leq 0.01$) correlation between estimates of GCA effects and mean performance of the parents was observed for a thousand grain weight (r = 0.96), panicle weight (r = 0.81), grain phenotypic acceptability (r = 0.84) and significant ($p<0.05$) correlation for weight of grains per panicle (r = 0.75). There was a significant correlation between GCA estimates for grain yield and mean for panicle weight (r = 0.74) and weight of grains per panicle (r = 0.76).

There was significant ($p<0.001$) positive correlation between SCA effects estimates and mean performance for grain yield (r = 0.91) (Table 5.17 above diagonal). Mean performance for grain yield was also significantly correlated with SCA estimates for all the other traits; negative with grain phenotypic acceptability only. Highly significant ($p<0.01$) and positive correlations were observed between SCA estimates for grain yield and means for spikelet fertility (r = 0.79), grains per panicle (r = 0.54), panicle weight (r = 0.44) and weight of grains per panicle (r=0.51). The other yield components also showed significant ($p<0.001$) and positive correction between mean performance and estimates of SCA effects with an exception of a thousand grain weight.

Table 5.17: Correlation coefficient of the estimate of SCA effects and mean of the F_3 populations (above diagonal) and GCA effect of and mean of the parent (below diagonal) for grain yield and yield components in the 10 x 10 half diallel cross of interspecific and *Oryza sativa* L. lines across environments

	GY†	**SF**	**TGWT**	**GPPN**	**PNWT**	**WTGPPN**	**GPACP**	**GYE**	**SFE**	**TGWTE**	**GPPNE**	**PNWTE**	**WTGPPNE**	**GPACPE**
GY		0.81***	-0.23	0.67***	0.42**	0.49**	-0.20	0.91***	0.78***	0.32*	0.67***	0.75***	0.71***	-0.51***
SF	0.22		-0.04	0.67***	0.48**	0.57***	-0.32*	0.79***	0.88***	0.15	0.68***	0.63***	0.65***	-0.60***
TGWT	0.15	0.59		-0.17	0.50**	0.47**	-0.65***	-0.06	-0.09	0.22	-0.17	-0.13	-0.08	-0.10
GPPN	-0.14	0.26	-0.02		0.63***	0.67***	-0.26	0.54***	0.56***	0.18	0.85***	0.62***	0.65***	-0.34*
PNWT	-0.20	0.52	0.78**	0.50		0.96***	-0.74***	0.44**	0.42**	0.23	0.53***	0.55***	0.57***	-0.41**
WTGPPN	-0.12	0.58	0.79**	0.49	0.99***		-0.72***	0.51***	0.50**	0.29	0.61***	0.61***	0.67***	-0.52***
GPACP	0.20	-0.44	-0.66*	-0.20	-0.80**	-0.84**		-0.28	-0.26	-0.26	-0.19	-0.25	-0.27	0.54***
GYE	0.23	-0.52	-0.59	-0.40	-0.74*	-0.76*	0.60		0.86***	0.29	0.63***	0.75***	0.72***	-0.53***
SFE	0.26	0.04	0.22	0.15	0.19	0.12	0.16	0.25		0.16	0.68***	0.72***	0.74***	-0.64***
TGWTE	0.13	0.64*	0.96***	-0.03	0.78**	0.79***	-0.71*	-0.60	0.15		0.14	0.39**	0.37*	-0.36*
GPPNE	0.16	-0.10	-0.31	0.59	-0.04	-0.07	0.20	0.44	0.52	-0.37		0.76	0.78	-0.48
PNWTE	-0.01	0.19	0.75*	0.26	0.81**	0.78**	-0.69*	-0.29	0.41	0.70*	0.18		0.95***	-0.61***
WTGPPNE	0.06	0.30	0.78**	0.15	0.77**	0.75*	-0.65*	-0.21	0.53	0.75*	0.20	-0.87**		-0.66***
GPACAE	0.08	-0.33	-0.69*	-0.33	-0.83**	-0.82**	0.84**	0.41	-0.27	-0.72*	-0.16	-0.90***	0.96***	

*, **, *** Significant at p< 0.05, 0.01 and 0.001 probability levels, respectively

† GY, Grain yield; SF, Spikelet fertility; TGWT, A thousand grain weight; GPPN**,** Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; GPACP, Grain phenotypic acceptability; E=stands for GCA or SCA effects for each traits

5.4 Discussion

5.4.1 Mean performance of genotypes

In this study significant variation among genotypes and environment main effects were observed for grain yield, spikelet fertility, a thousand grain weight, panicle weight, weight of grains per panicle and grain phenotypic acceptability. The variation observed among the genotypes and environments indicated that there was desirable genetic variation among the parents and their progenies for grain yield and all the other traits and that the environments in which these genotypes were grown were different. Moreover, the genotypes and the environments interacted, predisposing differential ranking of genotypes at each environment. Thus an appropriate breeding programme for these materials should allow for the development of genotypes with general and specific adaptation. The relative yield reduction under random drought stress compared to no drought stress at Msambweni long rain season control was only 18%. This indicated that the stress severity observed was mild and that yield potential was sufficient in sustaining yield under the random drought stress experienced at Msambweni short rain season. Such levels of yield reduction have also been reported under natural drought by other researchers (Lafitte *et al.*, 2004; Kumar *et al.*, 2008a; Kumar *et al.*, 2009). However, the relative drought index revealed differences in sensitivity to drought among the genotypes. The parent IR74371-54-1-1 had the highest relative drought index of 1.6 and this confirmed that it has high reproductive stage drought tolerance as reported by Verulkar *et al.* (2010). IR74371-54-1-1 appeared in three crosses that combined high yield potential with drought tolerance namely; NERICA-L-25 x IR74371-54-1-1 (1.26), Luyin 46 x IR74371-54-1-1 (1.0) and IR55423-01 x IR74371-54-1-1 (1.2). The drought tolerance observed in the local cultivar *Duorado* may have been contributed by its adaptability to the environments. Lack of drought tolerance expression in Vandana a line known to have a high reproductive drought tolerance (Venuprasad *et al.*, 2007) and in IR55423-01 a line with moderate drought tolerance (Venuprasad *et al.*, 2007) may have resulted from lack of adaptability to the environment.

Across environments, it was observed that Vandana appeared in five of the selected high yielding populations, indicating that this parent may have good combining ability for increased grain yield. Although the highest yielding population was Luyin 46 x IR55423-01, a cross between two high yielding parents, the major negative trait in this cross was grain phenotypic acceptability. Farmers in the region have a preference for heavy panicles, long and bold grains. The F_3 populations NERICA 1 x NERICA 2 and CT16323-CA-25-M x

Vandana combined high yield potential (4 t ha^{-1}) with moderate drought tolerance index (1). Outstanding F_3 populations which combined higher yields with higher thousand grain weight of over 30 g, heavy panicle weight of over 3.5 g, heavy grains per panicle of over 3.0 g and a good grain phenotypic acceptability score of 2 were NERICA 1 x NERICA 2, NERICA 1 x *Duorado* and NERICA 2 x *Duorado*. Of these, the cross NERICA 1 x NERICA 2, yielded significantly higher than the parents at each and across environments and had moderate relative drought index of 1.0. These NERICA varieties combine the best traits of high yields from the Asian parent (WAB 56-104) and the ability to thrive in harsh environments from the African parent (CG 14) (Semagn *et al.*, 2006). According to Semagn *et al.* (2006), euclidean distances for microsatellite and agronomic traits between NERICAs 1 and 2 ranged from 2.01 to 4.80. High yields in this cross may have resulted from the effect of complementary gene action towards increased grain yield in their progenies. This therefore suggests that through selection desirable transgressive segregates may be identified and advanced to homozygosity. Across environments, 86% of the selected high yielding F_3 populations were crosses between interspecific x *Oryza sativa* lines and vice versa, and between O*ryza sativa* L. lines, each with equal contribution. This suggests presence of favorable allele combinations between interspecific x *Oryza sativa* lines resulting to useful genetic variation in the F_3 populations.

5.4.2 Gene action

Significant GCA and SCA for grain yield and all the other traits were observed in this study indicating the importance of both additive and non-additive gene action in conditioning these traits. The only exception was a non-significant GCA for grain yield under random drought stress conditions suggesting the preponderance of non-additive gene action in conditioning grain yield under stress conditions. Further analysis of GCA/SCA predictability ratio (Baker, 1978) revealed that non-additive gene action was more important than additive gene action for grain yield, spikelet fertility, grains per panicle, and weight of grains per panicle under no drought and drought stress conditions. In contrast, additive gene action was more important for a thousand grain weight under no drought and drought stress condition. For panicle weight non-additive gene action was more important under no drought stress while both additive and non-additive gene action prevailed under drought stress. For grain phenotypic acceptability, additive gene action was more important under no drought stress while non-additive gene action prevailed under drought stress conditions. Several studies have reported the importance of non-additive gene effects in inheritance of grain yield (Kumar *et al.*, 2008b, Malarvizhi *et al.*, 2010; Dwivedi and Pandey, 2012), spikelet fertility and grains per panicle (Saidaiah and Ramesha, 2010; Dwivedi and Pandey, 2012). Expression of non-additive gene action either reduces or enhances selection limits, but in general it distorts predictions of genetic improvements (Kearsey and Pooni, 1996). However, its presence in these materials offers scope for exploitation of hybrid vigour through heterosis breeding in specific hybrid combinations. The predominance of additive gene action observed for a thousand grain weight in this study has also been reported by other researchers (Kumar *et al.*, 2007a; Kumar *et al.*, 2007b). Additive gene action due to joint effect of additive variance and additive x additive type of epistasis is fixable in the later generations. This, therefore suggests that a thousand grain weight and grain phenotypic acceptability can be improved through early generation selections and in simple recurrent selection aimed at accumulating desirable additive genes. Furthermore, this study revealed highly significant environmental effects and their interactions with GCA and SCA for grain yield and all the other traits measured, suggesting that GCA and SCA effects associated with parents and crosses respectively were not consistent over environments. Thus selection of parents and crosses should be matched to the selection site.

5.4.3 Combining ability effects

Estimation of combining ability effects provides knowledge of superior parents and a reasonable base for predicting the performance of yet untested crosses without making genetic assumptions (Simmonds, 1989). Superior parents may then be hybridized to exploit heterosis and to select better crosses for direct use or for further breeding work (Allard, 1960). The study identified *Oryza sativa* line Vandana as the best general combiner for grain yield and confirmed that it had good combining ability for increased grain yield as it appeared in five populations among the selected high yielding populations. Thus, Vandana exhibited more favourable alleles for grain yield. In support of these findings, a quantitative trait loci (QTL) analysis, using a F_3-derived population generated from the cross of upland rice (*Oryza sativa* L.) cultivars Vandana and Way Rarem, identified two loci from the Vandana genome; $qDTY_{2.3}$ on chromosome 2 and $qDTY_{3.2}$ on chromosome 3, that have positive effects on grain yield under upland and lowland conditions irrespective of stress levels (Dixit *et al.*, 2012). These researchers reported that lines with the Vandana alleles showed significantly higher yields (Dixit *et al.*, 2012). In addition to grain yield, Vandana was a good general combiner for spikelet fertility and in the previous chapter Vandana was also found to be a good general combiner for earliness. Other studies including the current study have shown that Vandana has high reproductive stage drought tolerance (Venuprasad *et al.*, 2007, Verulkar *et al.*, 2010). Therefore, Vandana stands out as a good candidate for improvement of grain yield and increased spikelet fertility in drought prone rainfed upland and lowland ecologies across sub-Saharan African countries. However, the major drawback in Vandana was the presence of undesirable alleles for the other yield components and grain phenotypic acceptability.

The line *Duorado* precoce had the best GCA effect for a thousand grain weight. The interspecific line NERICA 2 was the best for grains per panicle while NERICA 1 had the best GCA effects for panicle weight, weight of grains per panicle and grain phenotypic acceptability. NERICA 1 was good general combiner for all the undesirable traits found in Vandana. These lines therefore stand out as good candidates for improvement of these traits in drought prone rainfed upland and lowland ecologies across sub-Saharan African countries. The study revealed that SCA effects of crosses were independent of the GCA effects of the two parents. However, significant SCA effects would not be appreciated in this study since at the moment the rice breeding programme at the coastal lowlands of Kenya is not aiming to produce F_1 hybrids due to the cost implications involved.

5.4.4 Correlation of GCA and SCA estimates and mean of grain yield and the yield components

In this study, association between estimates of GCA effects and mean performance of the parents was non-significant for grain yield, spikelet fertility and grains per panicle. This suggested for these traits, the mean performance of the parents did not necessarily correspond with their GCA effects and could not be used as an indicator of their combining ability in hybrid combination. In contrast, there was a significant association between mean performance of parents and GCA effects for a thousand grain weight, panicle weight, grain phenotypic acceptability, and weight of grains per panicle indicating that for these traits, there was correspondence between mean performance of the parents and their GCA effects. Therefore, the mean performance of the parents was a good indicator of their combining ability in hybrid combination.

Furthermore, the association between mean performance of the F_3 populations and the SCA estimates was significant for grain yield and all the other traits with exception of a thousand grain weight. This suggested mean performance of the F_3 populations corresponded to their SCA effects. For example, high yielding F_3 populations also showed significant and positive SCA effects for grain yield. Therefore, both mean performance and SCA effects should be considered in judging the superiority of a cross.

5.5 Conclusions

This study revealed that the GCA and SCA effects were significant for grain yield and all the other traits suggesting the importance of both additive and non-additive gene action in conditioning these traits. However, further analysis of GCA/SCA predictability ratio (Baker, 1978) revealed that under stress and non-stress conditions non-additive gene action was more important than additive gene action for grain yield, spikelet fertility, number and weight of grains per panicle. In contrast, additive gene action was more important for a thousand grain weight. This suggests that for the traits conditioned by non-additive gene action selection of superior genotypes will be effective only in the later generations while for a thousand grain weight, this trait could be improved through recurrent selection. One line, Vandana, was found to be a good general combiner for grain yield contributing alleles for high grain yield to its progenies. The line *Duorado* precoce had the best GCA effect for a thousand grain weight. The interspecific line NERICA 2 was the best for grains per panicle while NERICA 1 had the best GCA effects for panicle weight, weight of grains per panicle and grain phenotypic acceptability. Thus these lines contributed desirable alleles for these traits to their progenies. For grain yield, spikelet fertility and grains per panicle the mean performance of the parents did not necessarily correspond with their GCA effects and could not be used as an indicator of their combining ability in hybrid combination. The F_3 populations NERICA 1 x NERICA 2 and CT16323-CA-25-M x Vandana combined high yield potential (4 t ha^{-1}) with moderate drought tolerance index (1). Outstanding F_3 populations which combined higher yields with a higher a thousand grain weight of over 30 g, heavy panicle weight of over 3.5 g, heavy grains per panicle of over 3.0 g and a good grain phenotypic acceptability score of 2 were NERICA 1 x NERICA 2, NERICA 1 x *Duorado* and NERICA 2 x *Duorado*. Of these, NERICA 1 x NERICA 2, yielded significantly higher than the parents at each and across environments and had a moderate relative drought index of 1.0. Among the selected high yielding F_3 populations 43% were crosses between interspecific x *Oryza sativa* lines and vice versa. This suggests presence of favorable allele combinations between interspecific x *Oryza sativa* lines resulting to useful genetic variation in the segregating populations.

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Appendices

Appendix A: Mean performance 45 F_3 populations and 10 diallel parents for grain yield at each and across no drought stress, under random managed drought stress and across environments and for relative drought index

F_3 populations	Grain yield						Relative drought index
	MTG	MTP	MSMLR	AC	MSMSR	AC	
	No drought stress				RMS		(RDI)
NERICA 1xCT16323-CA-25-M	3.68	3.74	2.55	3.32	2.90	3.22	1.14
NERICA 1xCT16333(1)-CA-22-M	4.18	3.47	3.11	3.58	3.12	3.47	1.00
NERICA 1x*Duorado*	3.64	2.22	3.39	3.08	5.01	3.56	1.48
NERICA 1xIR55423-01	3.49	3.00	2.46	2.98	3.65	3.15	1.48
NERICA 1xIR74371-54-1-1	2.38	2.80	4.04	3.07	3.52	3.18	0.87
NERICA 1xLuyin 46	2.72	2.66	3.15	2.84	1.55	2.52	0.49
NERICA 1xNERICA 2	4.45	4.15	3.95	4.18	4.08	4.15	1.03
NERICA 1xNERICA -L- 25	3.39	3.08	3.84	3.44	2.22	3.13	0.58
NERICA 1xVandana	4.04	2.19	4.94	3.72	2.46	3.40	0.50
NERICA 2xCT16323-CA-25-M	2.88	3.57	3.44	3.30	1.52	2.85	0.44
NERICA 2xCT16333(1)-CA-22-M	3.66	3.40	4.16	3.74	4.45	3.91	1.07
NERICA 2x*Duorado*	5.38	2.63	3.32	3.77	2.70	3.50	0.81
NERICA 2xIR55423-01	3.26	4.28	3.54	3.69	2.68	3.44	0.76
NERICA 2xIR74371-54-1-1	2.64	3.87	3.09	3.20	2.02	2.90	0.65
NERICA 2xLuyin 46	3.35	2.21	4.96	3.50	3.06	3.39	0.62
NERICA 2xNERICA -L- 25	2.24	3.04	4.50	3.26	3.86	3.41	0.86
NERICA 2xVandana	3.19	2.63	4.16	3.33	2.49	3.12	0.60
*Duorado*xCT16323-CA-25-M	3.97	3.16	2.46	3.19	3.92	3.37	1.60
*Duorado*xCT16333(1)-CA-22-M	5.07	3.12	2.14	3.44	3.48	3.45	1.63
*Duorado*xIR55423-01	3.06	2.23	2.53	2.61	1.60	2.35	0.63
*Duorado*xIR74371-54-1-1	2.39	3.27	2.37	2.68	2.19	2.55	0.92
*Duorado*xLuyin 46	2.13	3.76	3.34	3.07	1.98	2.80	0.59
*Duorado*xNERICA -L- 25	2.61	2.61	2.85	2.69	2.89	2.74	1.02
*Duorado*xVandana	3.13	2.67	2.82	2.87	2.43	2.76	0.86
CT16333(1)-CA-22-MxCT16323-CA-25-M	3.57	3.93	2.53	3.34	2.21	3.06	0.88
CT16333(1)-CA-22-MxIR55423-01	2.48	2.39	3.33	2.73	0.93	2.28	0.28
CT16333(1)-CA-22-MxIR74371-54-1-1	3.67	3.44	3.25	3.45	2.22	3.14	0.68
CT16333(1)-CA-22-MxLuyin 46	2.71	2.25	2.82	2.59	2.33	2.53	0.82
CT16333(1)-CA-22-MxNERICA -L- 25	2.71	2.65	2.37	2.58	3.94	2.92	1.67
CT16333(1)-CA-22-MxVandana	3.13	2.56	3.42	3.03	2.66	2.94	0.78
CT16323-CA-25-MxIR55423-01	2.91	2.82	2.57	2.76	2.86	2.79	1.11
CT16323-CA-25-MxIR74371-54-1-1	3.17	2.45	3.07	2.90	2.90	2.90	0.94
CT16323-CA-25-MxLuyin 46	2.68	2.21	3.40	2.76	2.53	2.70	0.75
CT16323-CA-25-MxNERICA -L- 25	2.26	3.02	2.96	2.74	3.93	3.04	1.33
CT16323-CA-25-MxVandana	4.44	3.36	4.20	4.00	4.04	4.01	0.96
Luyin 46xIR55423-01	4.35	3.00	6.46	4.60	4.32	4.53	0.67
Luyin 46xIR74371-54-1-1	2.05	3.79	4.64	3.49	4.60	3.77	0.99
Luyin 46xNERICA -L- 25	2.62	2.88	5.36	3.62	3.00	3.46	0.56
Luyin 46xVandana	4.78	2.29	6.91	4.66	2.92	4.23	0.42
NERICA -L- 25 xIR55423-01	3.55	4.93	4.14	4.20	3.19	3.95	0.77
NERICA -L- 25 xIR74371-54-1-1	3.19	4.49	3.49	3.72	4.06	3.81	1.16
NERICA -L- 25 xVandana	4.00	3.95	6.38	4.77	2.85	4.29	0.45
IR55423-01xIR74371-54-1-1	3.09	4.09	3.39	3.52	3.91	3.62	1.16
IR55423-01xVandana	3.27	4.32	3.81	3.80	3.78	3.79	0.99
VandanaxIR74371-54-1-1	5.12	3.98	3.68	4.26	2.88	3.91	0.78

Parents							
Interspecific lines							
NERICA 1	3.93	3.22	3.63	3.59	3.39	3.54	0.93
NERICA 2	3.63	3.28	3.63	3.51	3.47	3.50	0.96
CT16323-CA-25-M	3.78	3.45	2.24	3.16	3.32	3.20	1.48
CT16333(1)-CA-22-M	3.95	3.14	3.11	3.40	2.61	3.20	0.84
NERICA -L- 25	2.68	3.51	5.11	3.77	0.63	2.98	0.12
***Oryza sativa* L. lines**							
Vandana	4.43	3.26	4.79	4.16	3.05	3.88	0.64
Duorado	3.80	3.36	3.72	3.63	4.23	3.78	1.14
IR74371-54-1-1	2.62	4.41	2.50	3.18	3.88	3.35	1.55
Luyin 46	2.13	4.21	5.95	4.10	2.21	3.62	0.37
IR55423-01	4.61	3.73	3.73	4.02	2.36	3.61	0.63
Mean	**3.38**	**3.24**	**3.66**	**3.00**	**3.43**	**3.32**	**0.94**
Maximun	**5.12**	**4.93**	**6.91**	**4.77**	**4.60**	**4.53**	**1.67**
Minimum	**2.05**	**2.21**	**2.57**	**2.74**	**2.53**	**2.70**	**0.12**
LSD$_{(0.05)}$	**0.86**	**0.86**	**1.69**	**1.07**	**0.68**	**0.57**	**0.56**

Appendix B: Mean performance of the 45 F_3 populations and 10 diallel parents for yield components across environments

F_3 Populations	Yield components					
	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
NERICA 1xCT16323-CA-25-M	83.06	30.96	109.46	3.32	2.96	2.25
NERICA 1xCT16333(1)-CA-22-M	85.63	30.18	121.56	3.83	3.37	3.38
NERICA 1x *Duorado*	83.99	31.18	105.48	3.63	3.08	1.75
NERICA 1xIR55423-01	78.63	26.11	106.50	3.14	2.39	4.50
NERICA 1xIR74371-54-1-1	72.67	27.16	114.34	3.03	2.54	4.63
NERICA 1xLuyin 46	69.02	27.17	108.85	3.34	2.90	4.25
NERICA 1xNERICA 2	84.84	30.16	124.24	3.90	3.47	1.75
NERICA 1xNERICA -L- 25	74.02	24.41	120.48	3.12	2.58	5.50
NERICA 1xVandana	77.52	27.21	105.99	3.14	2.74	5.00
NERICA 2xCT16323-CA-25-M	79.44	30.13	120.55	3.65	3.25	2.38
NERICA 2xCT16333(1)-CA-22-M	86.12	30.55	119.84	3.72	2.89	3.75
NERICA 2x*Duorado*	75.46	33.45	108.45	3.78	3.15	2.00
NERICA 2xIR55423-01	78.47	24.74	114.10	2.95	2.49	5.38
NERICA 2xIR74371-54-1-1	63.68	27.84	108.11	2.95	2.39	4.63
NERICA 2xLuyin 46	74.07	26.93	113.25	3.35	2.88	4.13
NERICA 2xNERICA -L- 25	80.81	22.86	124.16	3.17	2.51	5.50
NERICA 2xVandana	76.17	27.56	118.10	3.29	2.77	4.38
*Duorado*xCT16323-CA-25-M	80.93	33.35	114.05	3.49	3.11	2.50
*Duorado*xCT16333(1)-CA-22-M	83.57	31.08	107.86	3.26	2.88	2.25
*Duorado*xIR55423-01	67.39	28.73	87.08	2.68	2.22	6.00
*Duorado*xIR74371-54-1-1	71.28	26.54	94.65	2.42	1.96	6.25
*Duorado*xLuyin 46	67.17	29.49	90.89	2.69	2.28	5.38
*Duorado*xNERICA -L- 25	59.86	26.15	99.13	2.53	1.93	5.75
*Duorado*xVandana	79.87	26.60	99.86	2.57	2.19	5.25
CT16333(1)-CA-22-MxCT16323-CA-25-M	81.70	32.30	105.34	3.20	2.79	2.25
CT16333(1)-CA-22-MxIR55423-01	62.76	27.67	96.00	2.68	2.10	4.88
CT16333(1)-CA-22-MxIR74371-54-1-1	74.74	27.54	113.48	3.26	2.76	4.13
CT16333(1)-CA-22-MxLuyin 46	68.60	26.52	97.21	2.59	2.09	5.88
CT16333(1)-CA-22-MxNERICA -L- 25	70.73	23.68	103.68	2.58	2.10	5.88
CT16333(1)-CA-22-MxVandana	72.88	26.03	103.34	2.78	2.37	5.00
CT16323-CA-25-MxIR55423-01	76.83	27.54	113.08	3.16	2.63	5.50
CT16323-CA-25-MxIR74371-54-1-1	74.03	26.65	98.98	2.63	2.20	4.88
CT16323-CA-25-MxLuyin 46	69.70	25.46	106.49	2.98	2.46	4.38
CT16323-CA-25-MxNERICA -L- 25	76.51	25.82	100.16	2.61	2.15	5.38
CT16323-CA-25-MxVandana	85.24	28.01	115.26	3.35	2.99	4.63
Luyin 46xIR55423-01	85.24	23.33	130.69	3.14	2.64	5.13
Luyin 46xIR74371-54-1-1	85.44	24.02	121.14	2.94	2.61	4.63
Luyin 46xNERICA -L- 25	75.71	23.26	107.53	2.80	2.41	4.88
Luyin 46xVandana	86.96	24.51	119.68	2.91	2.58	5.88
NERICA -L- 25 xIR55423-01	83.67	23.31	120.10	3.09	2.64	5.25
NERICA -L- 25 xIR74371-54-1-1	78.18	22.82	107.56	2.76	2.30	5.13
NERICA -L- 25 xVandana	80.00	22.93	108.65	2.86	2.49	6.75
IR55423-01xIR74371-54-1-1	82.77	23.20	139.24	3.44	2.99	5.38
IR55423-01xVandana	87.85	23.94	132.55	3.10	2.77	4.63
VandanaxIR74371-54-1-1	86.31	23.96	114.03	2.78	2.35	4.75

Parents						
Interspecific						
NERICA 1	85.70	29.65	125.29	4.16	3.75	1.00
NERICA 2	88.03	28.64	124.54	3.71	3.30	1.75
CT16323-CA-25-M	85.85	33.25	117.50	4.11	3.70	2.13
CT16333(1)-CA-22-M	89.85	31.04	130.80	4.27	3.83	1.75
NERICA -L- 25	71.02	21.12	99.38	2.28	1.88	4.75
Oryza sativa **L**						
Vandana	88.19	23.54	111.46	2.70	2.48	7.88
Duorado	91.88	35.74	117.30	4.04	3.71	1.00
IR74371-54-1-1	89.46	22.86	131.81	3.18	2.82	4.50
Luyin 46	80.67	23.03	122.13	2.79	2.51	4.88
IR55423-01	84.18	23.43	125.83	3.07	2.78	5.00
Across Entry mean	**78.81**	**27.01**	**112.68**	**3.14**	**2.69**	**4.33**
Maximun	**87.85**	**28.01**	**139.24**	**3.44**	**2.99**	**6.75**
Minimum	**69.70**	**22.82**	**98.98**	**2.61**	**2.15**	**4.38**
LSD$_{(0.05)}$	**6.76**	**1.82**	**14.40**	**0.44**	**0.41**	**0.85**
Matuga Mean	**75.97**	**25.40**	**104.12**	**2.87**	**2.50**	**4.36**
Mtwapa mean	**81.92**	**28.33**	**107.26**	**3.08**	**2.77**	**3.78**
Msambweni NDS	**83.57**	**27.83**	**136.63**	**3.75**	**3.15**	**4.31**
Msambweni RMS	**73.77**	**26.47**	**102.69**	**2.87**	**2.35**	**4.87**

Appendix C: The specific combining ability of F_3 populations for grain yield and yield components under random stress condition.

F_3 populations	GY	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
NERICA -L- 25 xIR74371-54-1-1	3.27***	27.88**	0.85	39.3	1.31**	1.22*	0.50
Luyin 46xIR74371-54-1-1	2.03***	1.37	2.01	22.65	1.24*	1.03*	-0.90
NERICA 1x *Duorado*	1.79***	11.65*	-1.11	2.71	0.29	-0.06	-0.42
NERICA 2xCT16333(1)-CA-22-M	1.63***	13.35*	-0.43	27.00**	0.05	-0.09	2.38**
Luyin 46xIR55423-01	1.55***	12.25*	-0.70	17.43	0.43	0.29	-1.12
IR55423-01xIR74371-54-1-1	1.26*	-10.04	-1.62	5.49	-0.32	-0.38	1.60
CT16333(1)-CA-22-MxNERICA -L- 25	1.10**	-2.90	-1.69*	20.76*	-0.45	-0.40	1.08
CT16323-CA-25-MxVandana	1.08**	8.00	-0.19	14.48	0.50	0.44	-0.82
IR55423-01xVandana	0.90*	4.58	0.34	31.08	0.39	0.51	-1.52*
NERICA 1xNERICA 2	0.87*	7.19	0.42	2.25	0.07	0.30	-0.32
*Duorado*xCT16323-CA-25-M	0.87*	7.09	1.53*	17.97*	0.23	0.39	-0.62
CT16323-CA-25-MxNERICA -L- 25	0.87*	6.10	0.03	-18.63*	-0.40	-0.47	1.18
NERICA 2xNERICA -L- 25	0.78*	6.38	-1.46	13.7	0.06	-0.01	-0.12
*Duorado*xIR74371-54-1-1	-2.22***	-17.57*	-3.16**	-30.10*	-0.85	-1.02*	5.30***
CT16333(1)-CA-22-MxIR55423-01	-1.79***	-18.20**	2.84**	-27.38**	-0.63*	-0.65*	0.98
NERICA 2xIR74371-54-1-1	-1.64**	-26.75**	0.89	9.76	-0.44	-0.59	1.2
NERICA 2xCT16323-CA-25-M	-1.51***	-10.65	1.12	-10.84	-0.22	-0.03	-0.52
NERICA 1xLuyin 46	-1.48***	-23.02***	0.22	-7.49	0.36	0.42	0.78
*Duorado*xIR55423-01	-1.36***	-26.52***	-1.86*	-34.69***	-0.79*	-0.74*	2.68***
NERICA 1xNERICA -L- 25	-1.02**	-0.64	0.26	17.02*	0.22	0.21	0.38
*Duorado*xLuyin 46	-0.91**	-18.39**	-1.16	-23.05**	-0.77*	-0.79*	1.18
NERICA 1xVandana	-0.68*	-11.83*	0.19	-15.53	-0.07	-0.07	1.38
*Duorado*xCT16333(1)-CA-22-M	0.65	16.22**	0.28	23.90**	0.73*	0.76*	-1.72*
NERICA 1xIR55423-01	0.54	1.77	-0.02	-15.63	-0.86**	-0.85**	-0.72
NERICA -L- 25 xIR55423-01	0.22	18.16**	1.86*	24.02	0.94**	1.02**	-0.52
NERICA 2xLuyin 46	0.18	0.09	0.16	-2.61	0.56	0.52	0.28
NERICA 1xCT16333(1)-CA-22-M	0.14	7.86	0.36	-14.19	0.18	0.01	-0.12
Luyin 46xVandana	0.13	4.77	1.11	10.11	-0.17	-0.1	0.98
NERICA 1xIR74371-54-1-1	0.10	-3.11	2.50*	-20.11	-0.19	-0.26	2.70*
Luyin 46xNERICA -L- 25	0.10	5.14	0.96	15.9	0.52	0.54	-1.02
CT16323-CA-25-MxIR55423-01	-0.07	-1.58	-0.34	-4.62	0.07	-0.33	1.08
CT16333(1)-CA-22-MxVandana	-0.09	-15.10**	-0.59	-18.98*	-0.26	-0.28	0.08
NERICA -L- 25 xVandana	-0.16	-2.92	0.13	-23.23	0.00	0.00	0.58
*Duorado*xNERICA -L- 25	-0.20	-7.48	-1.17	6.75	-0.19	-0.25	0.78
NERICA 2xIR55423-01	-0.27	1.05	-0.48	-9.24	-0.26	-0.3	0.78
NERICA 1xCT16323-CA-25-M	-0.3	1.02	-0.76	8.53	-0.24	-0.14	-0.02
CT16333(1)-CA-22-MxLuyin 46	-0.31	2.97	1.00	-16.00	-0.57	-0.59	0.48
CT16323-CA-25-MxLuyin 46	-0.32	-7.45	-1.41	-21.53*	-0.48	-0.55	0.58
NERICA 2x*Duorado*	-0.37	-2.06	1.35	-16.76*	-0.10	0.08	-0.92
VandanaxIR74371-54-1-1	-0.43	-11.14	-0.87	-10.62	-0.54	-0.57	-2.50*
NERICA 2xVandana	-0.49	-3.41	0.1	-4.54	-0.11	-0.20	-1.12
*Duorado*xVandana	-0.56	8.15	-0.16	5.76	-0.02	-0.07	-0.22
CT16333(1)-CA-22-MxCT16323-CA-25-M	-0.59	-8.33	-0.82	4.62	0.14	0.30	-1.32
CT16323-CA-25-MxIR74371-54-1-1	-0.63	-7.71	0.13	-30.67	-0.99*	-1.03*	0.90
CT16333(1)-CA-22-MxIR74371-54-1-1	-0.81	-13.45	0.28	-49.67***	-1.67**	-1.65**	3.00*

Appendix 5.4: The specific combining ability of F_3 populations for grain yield and yield components across no drought stress environments

F_3 Populations	GY	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
Luyin 46xIR55423-01	0.99**	7.04*	-0.03	13.22	0.20	0.16	-0.37
NERICA -L- 25 xVandana	0.84*	2.29	1.07	5.82	0.33	0.36	0.18
Luyin 46xVandana	0.68*	7.40*	0.67	5.81	0.22	0.21	-0.40
*Duorado*xIR74371-54-1-1	-1.19*	-23.91***	-2.42***	-35.98*	-1.64***	-1.78***	3.80***
CT16333(1)-CA-22-MxLuyin 46	-0.71*	-10.56**	-1.06	-11.47	-0.43	-0.49*	1.77***
*Duorado*xVandana	-0.68*	-3.01	-2.83***	-6.75	-0.49	-0.48*	0.67
CT16333(1)-CA-22-MxNERICA -L- 25	-0.68*	-4.16	-1.77**	-11.5	-0.25	-0.21	0.85*
NERICA 2xVandana	-0.67*	-7.53*	1.21	0.92	0.05	-0.01	0.13
NERICA 1xNERICA 2	0.66	3.96	0.54	5.07	0.12	0.21	-0.95**
NERICA -L- 25 xIR55423-01	0.64	4.59	1.25	0.51	0.19	0.24	-1.12**
VandanaxIR74371-54-1-1	0.61	6.86	0.91	5.03	0.29	0.12	-2.63***
*Duorado*xCT16333(1)-CA-22-M	0.56	5.14	-1.44*	1.85	-0.17	-0.04	-0.84*
NERICA 2x *Duorado*	0.53	-0.98	2.04***	6.02	0.48	0.29	-0.97**
NERICA 1xCT16333(1)-CA-22-M	0.42	6.19	-0.08	17.15	0.30	0.44	0.68*
NERICA 2xCT16333(1)-CA-22-M	0.41	6.07	0.95	-3.30	0.21	-0.08	0.13
CT16333(1)-CA-22-MxCT16323-CA-25-M	0.41	6.58	1.75**	-5.25	-0.25	-0.23	-0.72*
CT16323-CA-25-MxVandana	0.40	-0.07	0.25	0.73	0.19	0.18	0.28
*Duorado*xCT16323-CA-25-M	0.35	2.43	0.19	11.84	0.25	0.25	-0.49
NERICA 1xCT16323-CA-25-M	0.20	2.81	0.35	-6.79	-0.29	-0.21	-0.47
NERICA -L- 25 xIR74371-54-1-1	0.09	-3.49	1.03	-9.18	-0.01	-0.11	1.12*
NERICA 2xIR55423-01	0.06	-1.52	-2.08***	-7.67	-0.48	-0.34	1.17***
Luyin 46xNERICA -L- 25	0.02	1.67	1.31*	-7.24	0.07	0.12	-1.15***
NERICA 2xCT16323-CA-25-M	0.01	2.94	-1.11	10.03	0.17	0.24	-0.35
NERICA 1x *Duorado*	0.00	4.76	-0.43	-0.01	0.14	0.16	-1.25***
NERICA 1xNERICA -L- 25	-0.02	-2.99	-1.03	6.41	-0.08	-0.13	1.27**
CT16333(1)-CA-22-MxIR74371-54-1-1	-0.1	-15.92**	1.06	-12.45	-0.42	-0.58	0.87
NERICA 1xVandana	-0.11	-3.99	0.46	-7.14	-0.18	-0.18	0.35
NERICA 2xIR74371-54-1-1	-0.11	-22.41***	1.99**	-20.88	-0.19	-0.45	1.67**
*Duorado*xLuyin 46	-0.15	-3.32	1.45*	-7.63	-0.08	-0.07	1.00**
IR55423-01xVandana	-0.15	5.29	0.34	9.68	0.16	0.21	-1.54***
NERICA 2xLuyin 46	-0.16	-3.71	0.45	-4.71	-0.10	-0.06	-0.04
NERICA 2xNERICA -L- 25	-0.36	4.80	-2.26***	8.01	0.06	-0.06	1.22***
IR55423-01xIR74371-54-1-1	-0.36	2.69	0.41	18.97	0.74	0.50	0.33
Luyin 46xIR74371-54-1-1	-0.42	3.78	0.47	-12.26	-0.19	-0.14	0.03
CT16323-CA-25-MxIR74371-54-1-1	-0.46	-11.22*	-1.39*	-20.14	-1.23**	-1.22***	1.68**
CT16323-CA-25-MxNERICA -L- 25	-0.47	-1.67	-0.47	-3.29	-0.27	-0.26	0.53
CT16323-CA-25-MxIR55423-01	-0.47	-3.67	-0.05	-0.65	-0.05	-0.03	1.15***
NERICA 1xIR55423-01	-0.49	-2.61	-0.67	-11.26	-0.04	-0.39	0.72*
NERICA 1xIR74371-54-1-1	-0.49	-14.13**	0.36	-8.05	-0.74	-0.88*	1.95***
*Duorado*xNERICA -L- 25	-0.49	-15.09***	-0.82	-2.98	-0.27	-0.40	0.92**
CT16323-CA-25-MxLuyin 46	-0.5	-7.85*	-2.64***	2.51	0.01	-0.14	0.12
CT16333(1)-CA-22-MxIR55423-01	-0.54	-14.65***	0.05	-15.6	-0.42	-0.49*	-0.04
*Duorado*xIR55423-01	-0.58	-3.68	0.85	-15.15	-0.22	-0.21	1.03**
CT16333(1)-CA-22-MxVandana	-0.61	-6.62	-1.27	-3.78	-0.27	-0.26	0.10
NERICA 1xLuyin 46	-0.66	-3.80	0.49	-4.53	-0.07	-0.08	0.18

Appendix D: The specific combining ability of F_3 populations for grain yield and yield components across environments

F_3 Populations	GY	SF	TGWT	GPPN	PNWT	WTGPPN	GPACP
Luyin 46xIR55423-01	1.13***	8.34**	-0.26	13.68**	0.26	0.19	-0.56
NERICA 1xNERICA 2	0.71*	4.76	0.44	4.19	0.1	0.23	-0.79*
NERICA 2xCT16333(1)-CA-22-M	0.71*	7.89*	0.59	2.92	0.17	-0.08	0.69*
NERICA -L- 25 xVandana	0.59*	0.99	0.85	0	0.25	0.27	0.28
*Duorado*xIR74371-54-1-1	-1.45**	-22.32***	-4.22***	-12.89**	-1.45***	-1.59***	4.18***
NERICA 1xLuyin 46	-0.86**	-8.61**	0.37	-6.21	0.04	0.04	0.33
CT16333(1)-CA-22-MxIR55423-01	-0.85**	-15.54***	0.8	-20.18***	-0.47*	-0.53**	0.22
*Duorado*xIR55423-01	-0.78**	-9.39**	0.29	-21.78***	-0.36	-0.34	1.44***
*Duorado*xVandana	-0.65*	-0.22	-2.07**	-4.78	-0.37	-0.38	0.44
NERICA 2xVandana	-0.63*	-6.50*	0.82	0.31	0.01	-0.06	-0.18
CT16333(1)-CA-22-MxLuyin 46	-0.61*	-7.17*	-0.53	-14.71***	-0.47*	-0.51*	1.44***
NERICA -L- 25 xIR74371-54-1-1	0.89	4.35	0.09	-3.99	0.32	0.22	0.96
*Duorado*xCT16333(1)-CA-22-M	0.58	7.91*	-0.83	4.1	0.05	0.16	-1.06**
CT16323-CA-25-MxVandana	0.57	1.95	0.21	4.26	0.27	0.25	0.01
Luyin 46xVandana	0.54	6.74*	0.7	6.88	0.13	0.13	-0.06
NERICA -L- 25 xIR55423-01	0.53	7.98*	1.45	7.23	0.38	0.43*	-0.97**
*Duorado*xCT16323-CA-25-M	0.48	3.6	0.75	11.25*	0.25	0.29	-0.52
NERICA 1x *Duorado*	0.45	6.48*	-0.49	-1.42	0.17	0.11	-1.04**
NERICA 1xCT16333(1)-CA-22-M	0.35	6.61*	0.08	7.35	0.27	0.33	0.48
VandanaxIR74371-54-1-1	0.35	2.36	0.59	-1.7	0.08	-0.05	-2.60***
NERICA 2x *Duorado*	0.3	-1.25	1.91*	-1.15	0.34	0.24	-0.96**
Luyin 46xIR74371-54-1-1	0.19	3.18	1.1	5.44	0.16	0.15	-0.2
CT16333(1)-CA-22-MxCT16323-CA-25-M	0.16	2.85	1.28	-4.79	-0.15	-0.1	-0.87*
IR55423-01xVandana	0.11	5.11	0.3	15.50***	0.22	0.29	-1.53***
NERICA 1xCT16323-CA-25-M	0.08	2.36	0.17	-3.79	-0.28	-0.19	-0.36
IR55423-01xIR74371-54-1-1	0.05	-0.49	-0.29	19.29***	0.48	0.28	0.65
Luyin 46xNERICA -L- 25	0.04	2.54	1.23	-1.09	0.18	0.23	-1.12***
NERICA 2xIR55423-01	-0.02	-0.88	-1.76*	-7.91	-0.42	-0.33	1.07**
NERICA 2xLuyin 46	-0.07	-2.76	0.26	-4.51	0.06	0.09	0.04
NERICA 2xNERICA -L- 25	-0.07	5.19	-2.08**	10.55*	0.06	-0.05	0.88**
CT16323-CA-25-MxNERICA -L- 25	-0.14	0.27	-0.18	-6.65	-0.31	-0.31	0.69*
NERICA 1xIR55423-01	-0.23	-1.52	-0.52	-12.81**	-0.25	-0.50*	0.36
CT16333(1)-CA-22-MxNERICA -L- 25	-0.24	-3.84	-1.63*	-4.1	-0.3	-0.26	0.91**
NERICA 1xVandana	-0.25	-5.95	0.35	-9.1	-0.15	-0.15	0.61
NERICA 1xNERICA -L- 25	-0.27	-2.4	-0.66	9.57*	0	-0.04	1.04**
CT16333(1)-CA-22-MxIR74371-54-1-1	-0.28	-15.30**	-0.1	-1.38	-0.73*	-0.85**	1.40**
NERICA 1xIR74371-54-1-1	-0.34	-11.37*	0.67	-3.65	-0.6	-0.72*	2.14***
*Duorado*xLuyin 46	-0.34	-7.09*	0.87	-13.72**	-0.25	-0.25	1.04**
NERICA 2xCT16323-CA-25-M	-0.37	-0.46	-0.51	4.59	0.07	0.17	-0.39
CT16323-CA-25-MxIR55423-01	-0.37	-3.14	-0.02	-2.14	-0.02	-0.11	1.13**
*Duorado*xNERICA -L- 25	-0.42	-13.19***	-0.73	-1.33	-0.25	-0.36	0.88**
CT16323-CA-25-MxLuyin 46	-0.46	-7.75*	-2.27**	-4.48	-0.11	-0.25	0.23
CT16333(1)-CA-22-MxVandana	-0.48	-8.74**	-1.08	-8.62	-0.27	-0.27	0.09
NERICA 2xIR74371-54-1-1	-0.49	-23.49***	2.22	-12.58*	-0.25	-0.49	1.55**
CT16323-CA-25-MxIR74371-54-1-1	-0.50	-10.35*	-2.52*	-14.92***	-1.17***	-1.17***	1.49**

Chapter Six

Heritability, correlation and path coefficient analysis for grain yield and yield components in rice

Abstract

Although the main breeding objective in all crops is high yield, direct selection for yield is not sufficiently effective due to its low heritability. The use of secondary traits as indirect selection criteria for higher yields has often been suggested. The objective of this study was to determine heritability estimates, character associations, direct and indirect effects of individual characters on grain yield, and identity phenological, morphological and yield components that could be used in grain yield improvement. Five interspecific and five *Oryza sativa* L. lines were mated in half- diallel mating design and the resulting F_1 progenies advanced to F_3 generation. The 45 F_3 populations, their parents and one check were evaluated in 7 x 8 alpha lattice design with two replications. The materials were evaluated under three no drought and one random managed drought stress condition at three sites in coastal lowlands of Kenya. The traits measured were days to heading, anthesis and maturity, number of productive tillers per plant, plant height, a thousand grain weight, grains per panicle, panicle weight, weight of grains per panicle, grain phenotypic acceptability and grain yield. Narrow sense heritability estimates were high for days to heading (67%), days to anthesis (69%), days to maturity (90%) and a thousand grain weight (82%) indicating predominance of additive gene action and that the traits may be improved through recurrent selection procedures aimed at increasing gene frequencies of the favourable alleles. Narrow sense heritability estimates were very low for grain yield (0.1%) and the other yield components; spikelet fertility (4%), number of grains per panicle (16%), panicle weight (0.7%) and weight of grains per panicle (0.5%) suggesting predominance of non-additive gene action and that selection based on these traits may not be effective in early generations but in the later generations. Direct effects on grain yield were significant and positive for number of productive tillers per plant (P = 0.71), panicle weight (P = 0.66) and spikelet fertility (P = 0.49). Thus these traits may be used for direct selection of grain yield, but in later generation because they exhibited low to moderate narrow sense heritability estimates. A thousand grain weight had a high narrow sense heritability (82%) and positive indirect effect (P = 0.44) on grain yield via panicle weight indicating that improvement of grain yield may begin in early generations by indirectly selecting for higher a thousand grain weight via heavy panicle weight.

Keywords: Narrow sense heritability, rice, correlation and path coefficient analysis, grain yield

6.1 Introduction

Heritability is the proportion of observed phenotypic variation in a progeny that is attributable to the effects of genes (i.e. heritable) (Kearsey and Pooni, 1996, Sleper and Poehlman, 2006). Heritability of a trait is influenced by the number of genes involved, the population and the environment. Altering one of these factors results in different estimates of heritability (Acquaah, 2007). Although there are two different estimates of heritability, broad and narrow sense heritability, the latter which is the degree of resemblance between relatives is more useful to plant breeders. This is because it determines inheritance of a character from parent to offspring, best selection method for improvement of that character and prediction of genetic advance (Sleper and Poehlman, 2006). High narrow sense heritability estimates correspond to additive gene action while low heritability estimates are indicative of non-additive gene action. Moreover, a trait with high narrow sense heritability estimates indicates that the transmissibility of that trait from the parents to the progeny is high and that simple selection procedures may be employed to select for superior genotypes and *vice versa* (Sleper and Poehlman, 2006).

Grain yield is regarded as the primary character with the main breeding objective in all crops being high yields. However, direct selection for yield is not sufficiently effective due to its low heritability. The use of phenological, morphological and physiological traits commonly known as secondary traits, as indirect selection criteria for higher yields has often been suggested. In rice, correlation studies have identified traits associated with grain yield that may be effectively used to improve grain yield. Significant and positive associations of grain yield have been observed with spikelet fertility, a thousand grain weight and number of grains per panicle under water stress conditions (Babu *et al.*, 2003; Zou *et al.*, 2005; Bernier *et al.*, 2007; Sellamuthu *et al.*, 2011); number of filled grains per panicle under no drought conditions (Surek and Beser, 2003); and number of productive tillers per plant (Surek and Beser, 2003; Akinwale *et al.*, 2011). In contrast, significant and negative association of grain yield with days to heading and days to flowering has been observed under non stress conditions (Augustina *et al.*, 2013). Most of the literature reviewed suggests that in rice, spikelet fertility is a major contributor of grain yield especially under aerobic conditions.

Although correlation coefficients are very important in determining the relative contribution of each trait to grain yield, they are insufficient in determining whether the traits affect grain yield directly or indirectly (Nandan *et al.*, 2010). Through path analysis, the correlation coefficient may be partitioned into component due to direct effect of a predictor variable upon its response variable and component due to indirect effect(s) of a predictor variable on the response variable through another predictor variable (Dewey and Lu, 1959). Plant breeders use path analysis to identify traits that are useful as selection criteria to improve crop yield (Surek and Beser, 2003). Research done has shown that positive and direct effects on grain yield were mostly of number of productive tillers (Ibrahim *et al.*, 1990; Babu *et al.*, 2012; Seyoum *et al.*, 2012); panicle weight (Samonte *et al.*, 1998); and spikelet fertility (Zou *et al.*, 2005; Seyoum *et al.*, 2012; Hasan *et al.*, 2014).

Forward selection multiple regression analysis has been used to analyse traits of economic importance in cassava (Afuape *et al.*, 2011) and in rice (Augustina *et al.*, 2013). This model identifies which trait came into the model and left the model significant after regression with the dependent trait (yield), starting from the trait with the highest R-Squared and followed by progressive addition of new traits that increase the R-Squared the most (Bendel and Afifi, 1977). The selection stops when none of the remaining variables are significant (Bendel and Afifi, 1977). Augustina *et al.* (2013) also used forward selection multiple regression analysis to identify traits that would most contribute to grain yield improvement in a rice breeding programme. Number of grains per plant, weight of roots and days to 50% heading were identified as the most important yield components that could improve rice yields.

In the coastal region of Kenya a rice breeding programme aimed at developing high yielding, short duration cultivars with desired plant height for the rainfed upland and lowland ecologies in the region started in 2012. The breeding programme is utilizing early maturing interspecific lines from the African Rice Centre (ARC) and the International Centre for Tropical Agriculture (CIAT and high yielding *Oryza sativa* lines from the International Rice Research Institute (IRRI). Crosses between these interspecific and *Oryza sativa* lines were made and advanced to F_3 generation. However, although genetic studies on earliness and grain yield have been conducted, information on the contribution and effect of phenological, morphological and yield components on grain yield in these materials is lacking. Therefore, the objective of this study was to determine a) heritability estimates; b) character associations and c) direct and indirect effects of individual characters on grain yield; d) identify potential phenological, morphological and yield components that could be used in grain yield improvement while advancing selected F_3 populations to homozygozity.

6.2 Materials and methods

6.2.1 Germplasm, experimental sites, design and management

Description of the rice lines used in the 10x10 half diallel mating are presented in Chapter 4. section 4.2.2. The experimental sites, experimental layout and management, have all been described in chapter 4 section 4.2.1 and 4.2.3 to 4.2.6

6.2.2 Data collection

The Standard Evaluation System (SES) for rice reference manual (IRRI, 1996) was used for all traits measured except where stated. Thirty six plants were randomly selected and tagged for data collection. On each plant, data were collected on days to heading (DH), days to anthesis, days to maturity, plant height, tiller number, spikelet fertility, one thousand grain weight, number of grains per panicle, weight of panicle, weight of grains per panicle, and grain phenotypic acceptability and grain yield. Details of these traits are given in chapter 4 section 4.2.9 and in chapter five section 5.2.2.

6.2.3 Data analysis

The genetic variances for the various traits was calculated as follows: Genetic variance (Vg) = (genotypic mean squares – error mean squares)/number of replicates; Phenotypic variance (Vp) as the sum total of the genotypic variance and environmental variance (Vp = Vg + Ve). The genotypic coefficient of variation (CVG) =(√vg/grand mean)*100; Phenotype coefficient of variation (CVP) =(√vp/grand mean)*100; Broad-sense heritability (h_b^2): $\frac{\hat{\sigma}^2\mathrm{GCA}+\hat{\sigma}^2\mathrm{SCA}}{\hat{\sigma}^2\mathrm{phenotypic}}$; Narrow-sense heritability (h_n^2): $\frac{\hat{\sigma}^2\mathrm{GCA}}{\hat{\sigma}^2\mathrm{phenotypic}}$.; The variances for calculating broad and narrow sense heritability's were computed from Griffing's method 2 random effects model as suggested by Zhang, et al., 2005.

Phenotypic correlation coefficients were calculated for comparisons among the studied characters. Path co-efficient analysis between paddy yield and pheno-morphological traits and yield components was made using PATHSAS: the SAS computer program for path coefficient analysis of quantitative data as described by Cramer and Wehner (1999) in SAS (SAS Institute, 2012). Stepwise multiple regression analysis was carried out using GenStat statistical package version 14 (Payne *et al.*, 2011).

6.3 Results

Results on relative yield reduction under random drought stress compared to no drought stress at Msambweni long rain season (control) showed that the stress severity observed in this study was mild. Therefore heritability estimates, correlation and path analysis for all traits measured was computed across environments.

6.3.1 Heritability estimates and genetic variability

The phenotypic coefficient of variation (PCV) was higher than genotypic coefficient of variation (GCV) for all the characters studied (Table 6.1). The GCV was highest for grains per panicle (22.59) followed by spikelet fertility (16.02) and lowest for panicle weight (1.15), weight of grains per panicle (1.43) and grain yield (1.70). The broad sense heritability estimates were larger than the narrow sense heritability estimates. The differences in broad and narrow sense heritability estimates were larger for spikelet fertility and grains per panicle. Broad sense heritability estimates were above 80% for phenological traits, a thousand grain weight, grains per panicle and spikelet fertility. Based on the categories of narrow sense heritability, where low < 0.2, moderate 0.2 to 0.4 and high > 0.4; the estimates were high for days to heading (67%), days to anthesis (69%), days to maturity (90%) and a thousand grain weight (82%); moderate for tiller number (29%) and phenotypic acceptability (28%) and low for all the remaining traits including grain yield with 0.09%.

Table 6.1: Variance components, coefficient of variation and heritability in broad and narrow sense across environments

Traits	Variance components		Coefficient of variation		Heritability broad sense (%)	Heritability narrow sense (%)
	Phenotypic	Genotypic	Phenotypic	Genotypic		
DH†	23.23	22.32	6.24	6.11	85.70	67.35
DA	27.91	26.91	6.60	6.48	86.34	68.63
DM	43.59	43.09	6.15	6.12	92.67	89.53
TNO	0.46	0.18	7.67	4.81	29.72	28.94
PH	14.27	7.90	3.79	2.82	25.36	15.03
GPACP	0.23	0.14	11.19	8.68	36.23	28.17
TGWT	5.27	4.85	8.50	8.15	82.98	82.40
GPPN	674.69	648.02	23.05	22.59	80.90	16.07
PNWT	0.03	0.00	5.11	1.15	1.24	0.69
WTGPPN	0.02	0.00	5.69	1.43	1.30	0.51
SF	165.22	159.34	16.31	16.02	80.94	4.26
GY	0.05	0.00	6.44	1.70	0.82	0.09

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; TNO, Tiller numbers; PH, Plant height; GPACP, grain phenotypic acceptability; TGWT, A thousand grain weight; GPPN, Grains per panicle; PNWT, Panicle weight; WTGPPN, Weight of grains per panicle; SF, Spikelet fertility; GY, Grain yield

6.3.2 Phenotypic correlation coefficient analysis of grain yield, phenology and yield components

Results of phenotypic correlations between grain yield, phenological traits and yield components are presented in Table 6.2. There were highly significant ($P<0.01$) and positive association between grain yield and spikelet fertility ($r = 0.75$), grains per panicle ($r = 0.62$), weight of grains per panicle ($r = 0.44$) and panicle weight (0.36) and a significant and positive associations between grain yield and tiller number ($r = 0.32$). The association between grain yield and phenological traits were positive and non-significant. Moreover, a thousand grain weight and phenotypic acceptability were negatively associated with grain yield but the association was non-significant. There was a highly significant and positive association between days to heading and days to anthesis ($r = 0.97$), days to maturity ($r = 0.83$) and tiller number ($r = 0.49$) and a significant and negative association between days to heading and a thousand grain weight ($r = -0.56$) and panicle weight ($r = -0.27$). Further, highly significant and positive association was observed between spikelet fertility and grains per panicle ($r = 0.72$), weight of grains per panicle ($r = 0.64$) and panicle weight ($r = 0.55$). In contrast a significant and negative association was observed between spikelet fertility and phenotypic acceptability.

Table 6.2: Phenotypic correlation coefficients between grain yield and phenological, morphological and yield components across environments

	GPACP	WTGPPN	PNWT	GPPN	TGWT	SF	PH	TNO	DM	DA	DH	GY
GPACP		-0.76***	-0.78***	-0.33*	-0.66***	-0.39**	0.30*	0.52***	0.39**	0.15	0.17	-0.15
WTGPPN			0.97***	0.69***	0.55***	0.64***	-0.15	-0.51***	-0.37**	-0.19	-0.21	0.44**
PNWT				0.63***	0.59***	0.55***	-0.15	-0.59***	-0.36**	-0.24	-0.27*	0.36**
GPPN					-0.10	0.72***	-0.12	0.04	0.11	0.21	0.22	0.62***
TGWT						0.09	-0.10	-0.81***	-0.66***	-0.54***	-0.56***	-0.18
SF							0.08	0.01	-0.17	0.02	0.00	0.75***
PH								0.22	0.05	0.01	0.02	0.19
TNO									0.49***	0.46***	0.49***	0.32*
DM										0.82***	0.83***	0.07
DA											0.97***	0.17
DH												0.18

† DH, Days to heading; DA, Days to anthesis; DM, Days to maturity; PH, Plant height; TNO, Tiller numbers; GPPN, Grains per panicle; GY, Grain yield; GPACP, grain phenotypic acceptability; PNWT, Panicle weight; SF, Spikelet fertility; TGWT, A thousand grain weight; WTGPPN, Weight of grains per panicle

6.3.3 Path coefficient analysis

The direct and indirect effects of phenological, morphological and yield component characters along with their correlation coefficients with grain yield are presented in Table 6.3. There were highly significant ($p \leq 0.001$) and positive direct effects of number of productive tillers per plant (P = 0.71) and spikelet fertility (P = 0.49) on grain yield. The contribution of direct effects of spikelet fertility and tiller number on grain yield was 28% and 21%, respectively. Direct effects of panicle weight (P = 0.66) and days to anthesis (P = 0.41) on grain yield were also high and positive though not significant. Direct effects of days to heading (P = -0.59), weight of grains per panicle (P = -0.31) and a thousand grain weight (P = -0.15) on grain yield were negative. The direct effects of the remaining characters on grain yield were positive and very low ranging from P = 0.05 to P = 0.10.

The indirect effects on grain yield via spikelet fertility were all positive with exception of negative indirect effects of days to maturity. However, grains per panicle (P = 0.35), panicle weight (P = 0.28) and weight of grain per panicle showed the highest positive indirect effects on grain yield via spikelet fertility. Spikelet fertility (P = 0.38), a thousand grain weight (P = 0.44), number of grains per panicle (P = 0.40) and weight of grains per panicle (P = 0.65) showed positive indirect effects on grain yield via panicle weight. Days to heading (P = 0.41), days to maturity (P = 0.36) and tiller number (P = 0.22) had indirect effects on grain yield through days to anthesis. Again, days to heading (P = 0.39), days to anthesis (P = 0.37), days to maturity (P = 0.35) had positive indirect effects on grain yield which could be justified through tiller number per plant. Further, spikelet fertility (P = 0.38), a thousand grain weight (P = 0.44), number of grains per panicle (0.40), and weight of grains per panicle (P = 0.65) had positive indirect effects through panicle weight. Spikelet fertility (P = 0.20) once again had a positive indirect effect via weight of grains per panicle and a thousand grain weight (P = 0.32) had a positive indirect effect via days to heading.

In contrast, negative indirect effects on grain yield were observed for days to anthesis (P = -0.58), days to maturity (P = -0.51), tiller number (P = -0.32) and grains per panicle (P = -0.19) through days to heading; a thousand grain weight (P = -0.55), panicle weight (P = -0.39) and weight of grains per panicle (P = 0.34) via tiller number and also via weight of grains per panicle. The other indirect effects via the different characters on grain yield were negligible

Table 6.3: Phenotypic path coefficient showing direct and indirect effects of different components on grain yield across four environments

Effects	Path coef.	% Con.
DH VS GY	0.21	
Direct effect	-0.59	0.21
Indirect effect via DA	-0.58	0.20
Indirect effect via DM	-0.51	0.18
Indirect effect via TNO	-0.32	0.11
Indirect effect via PH	0.06	0.02
Indirect effect via SF	-0.04	0.01
Indirect effect via TGWT	0.32	0.11
Indirect effect via GPPN	-0.19	0.07
Indirect effect via PNWT	0.13	0.05
Indirect effect via WTGPPN	0.11	0.04
DA VS GY	0.21	
Direct effect	0.41	0.21
Indirect effect via DH	0.41	0.21
Indirect effect via DM	0.36	0.18
Indirect effect via TNO	0.22	0.11
Indirect effect via PH	-0.05	0.03
Indirect effect via SF	0.02	0.01
Indirect effect via TGWT	-0.22	0.11
Indirect effect via GPPN	0.13	0.07
Indirect effect via PNWT	-0.09	0.05
Indirect effect via WTGPPN	-0.08	0.04
DM VS GY	0.08	
Direct effect	0.10	0.19
Indirect effect via DH	0.09	0.17
Indirect effect via DA	0.09	0.17
Indirect effect via TNO	0.05	0.10
Indirect effect via PH	-0.01	0.02
Indirect effect via SF	-0.02	0.04
Indirect effect via TGWT	-0.06	0.12
Indirect effect via GPPN	0.02	0.04
Indirect effect via PNWT	-0.04	0.08
Indirect effect via WTGPPN	-0.04	0.08
TNO VS GY	0.44*	
Direct effect	0.71***	0.21
Indirect effect via DH	0.39	0.12
Indirect effect via DA	0.37	0.11
Indirect effect via DM	0.35	0.11
Indirect effect via PH	0.08	0.02
Indirect effect via SF	0.06	0.02
Indirect effect via TGWT	-0.55	0.17
Indirect effect via GPPN	0.08	0.02
Indirect effect via PNWT	-0.39	0.12
Indirect effect via WTGPPN	-0.34	0.10
PH VS GY	0.15	
Direct effect	0.05	0.50
Indirect effect via DH	-0.01	0.10
Indirect effect via DA	-0.01	0.10
Indirect effect via DM	0.00	0.00
Indirect effect via TNO	0.01	0.10
Indirect effect via SF	0.01	0.10
Indirect effect via TGWT	0.00	0.00
Indirect effect via GPPN	-0.01	0.10
Indirect effect via PNWT	0.00	0.00
Indirect effect via WTGPPN	0.00	0.00
SF VS GY	0.74***	
Direct effect	0.49***	0.28
Indirect effect via DH	0.03	0.02
Indirect effect via DA	0.03	0.02
Indirect effect via DM	-0.08	0.05
Indirect effect via TNO	0.04	0.02
Indirect effect via PH	0.05	0.03
Indirect effect via TGWT	0.06	0.03
Indirect effect via GPPN	0.35	0.20
Indirect effect via PNWT	0.28	0.16
Indirect effect via GPACP	0.32	0.18
TGWT VS GY	-0.15	
Direct effect	0.06	0.19
Indirect effect via DH	-0.03	0.10
Indirect effect via DA	-0.03	0.10
Indirect effect via DM	-0.04	0.13
Indirect effect via TNO	-0.05	0.16
Indirect effect via PH	0.00	0.00
Indirect effect via SF	0.01	0.03
Indirect effect via GPPN	-0.01	0.03
Indirect effect via PNWT	0.04	0.13
Indirect effect via WTGPPN	0.04	0.13
GPPN VS GY	0.63***	
Direct effect	0.05	0.23
Indirect effect via DH	0.02	0.09
Indirect effect via DA	0.02	0.09
Indirect effect via DM	0.01	0.05
Indirect effect via TNO	0.01	0.05
Indirect effect via PH	-0.01	0.05
Indirect effect via SF	0.03	0.14
Indirect effect via TGWT	-0.01	0.05
Indirect effect via PNWT	0.03	0.14
Indirect effect via WTGPPN	0.03	0.14
PNWT VS GY	0.32**	
Direct effect	0.66*	0.19
Indirect effect via DH	-0.15	0.04
Indirect effect via DA	-0.14	0.04
Indirect effect via DM	-0.24	0.07
Indirect effect via TNO	-0.37	0.11
Indirect effect via PH	-0.06	0.02
Indirect effect via SF	0.38	0.11
Indirect effect via TGWT	0.44	0.13
Indirect effect via GPPN	0.40	0.11
Indirect effect via WTGPPN	0.65	0.19
WTGPPN VS GY	0.37**	
Direct effect	-0.31	0.19
Indirect effect via DH	0.06	0.04
Indirect effect via DA	0.06	0.04
Indirect effect via DM	0.12	0.07
Indirect effect via TNO	0.15	0.09
Indirect effect via PH	0.02	0.01
Indirect effect via SF	-0.20	0.12
Indirect effect via TGWT	-0.20	0.12
Indirect effect via GPPN	-0.20	0.12
Indirect effect via PNWT	-0.30	0.19

6.3.4 Regression analysis

Forward selection multiple regression analysis showed that 73% of the total variation in grain yield could be explained by the variation in spikelet fertility, tiller number per plant and panicle weight. Spikelet fertility alone explained 54% of the total variation in grain yield.

Table 6.4: Forward selection multiple regression analysis between grain yield and other traits that were significant ($p<0.01$) in the multiple regression model

Variable entered	No of variables	Regression equation	R^2	F value	Pr>F
Spikelet fertility	1	GY = -0.609 + 0.050 SF	53.70	109.02	<.001
Tiller number	2	GY = -1.543 + 0.477 SF + 0.126 TNO	67.90	29.04	<.001
Panicle weight	3	GY = -2.285 + 0.035 SF + 0.270 TNO + 0.441 PNWT	72.80	10.26	0.002

6.4 Discussion

The broad sense heritability or repeatability was high (above 80%), for days to heading, days to anthesis, days to maturity, a thousand grain weight, grains per panicle and spikelet fertility. High repeatability and therefore heritability indicates that progress may be made in improvement of these traits. The broad sense heritability estimates for phenological traits were similar to those reported by Babu *et al.* (2003) and (Akinwale *et al.*, 2011). In contrast broad sense heritability estimates were very low (1%) for panicle weight, weight of grains per panicle and grain yield. Low repeatability indicates that little progress will be made in improvement of these traits. The broad sense heritability estimates for grain yield observed in this study were lower than those observed in other studies (Babu *et al.*, 2003, Kumar *et al.*, 2007, Verulkar *et al.*, 2010; Venuprasad *et al.*, 2007; Bernier *et al.*, 2009; Yue *et al.*, 2005); For example, Babu *et al.* (2003) reported broad sense heritability estimates of 59% under drought stress and 61% under no drought stress conditions. Kumar *et al.* 2007 reported estimates of 37% and 45% under severe and control conditions. Studies by Venuprasad *et al.* 2007 reported that broad sense heritability estimates for rice yield at reproductive stage under non-stress and stress conditions were 43% and 67%, respectively.

The narrow sense heritability estimates for days to heading (67%), days to anthesis (69%) and days to maturity (90%) were high confirming that a major portion of the phenotypic variance for phenological traits was contributed by additive gene action. High levels of heritability estimates suggested that selection for desired phenology under drought and no drought environments was likely. In addition, simple selection procedures based on GCA may be employed to enhance development of drought escaping cultivars adapted to the rainfed upland and lowland ecosystems in coastal lowlands of Kenya spilling over to sub-Saharan Africa. The narrow sense heritability estimates for number of productive tillers per plant were moderate (29%) and low for plant height (15%). Number of productive tillers could be increased through selection. However, selection for the desired plant height may have to wait until the later generations when homozygozity has set in. Among the yield components, the narrow sense heritability was high for a thousand grain weight only, indicating predominance of additive gene action and that the trait could be effectively improved through selection. The narrow sense heritability estimates for the other yield components; spikelet fertility (4%), number of grains per panicle (16%), panicle weight (0.7%) and weight of grains per panicle (0.5%) were very low. Low narrow sense heritability was also observed for grain yield (0.1%). The low heritability estimates for yield and other yield components with exception of a thousand grain weight supported the involvement of non-additive gene action in the inheritance of these traits as reported in chapter 5 and suggests that hybridization can be a choice for developing hybrids with high yield and desired attributes for the other yield components. It also suggests that selection based on these traits is not effective in early generations but in the later generations.

Besides, this study showed that grain yield had a positive and significant association with spikelet fertility (r = 0.75), grains per panicle (r = 0.62), weight of grains per panicle (r = 0.44) panicle weight (r = 0.36) and number of productive tillers per plant (r = 0.32). This necessitated further analysis to determine the direct and indirect effects of each trait on grain yield. Maximum positive and significant direct effects on grain yield were recorded for number of productive tillers per plant (P = 0.71), panicle weight (P = 0.66) and spikelet fertility (P = 0.49). Moreover, forward selection multiple regression analysis results showed that these three traits were the major contributors of increased yield in the materials under study. This implied that high yielding genotypes had higher number of productive tillers per plant, heavy panicle weight and high percentage of spikelet fertility. Thus the traits may be used for direct selection of grain yield. These findings concur with other researchers who reported that direct effects on grain yield in rice were mostly of number of productive tillers per plant (Ibrahim *et al.*, 1990; Babu *et al.*, 2012; Seyoum *et al.*, 2012), panicle weight (Samonte *et al.*, 1998) and spikelet fertility (Zou *et al.*, 2005; Seyoum *et al.*, 2012; Hasan *et al.*, 2014). In contrast to findings in this current study, a study on forward multiple regression analysis indicated that number of grains per panicle was the major contributor to yield improvement in rice (Augustina *et al.*, 2013).

High and positive indirect effects on grain yield were observed for weight of grains per panicle (P = 0.65), a thousand grain weight (P = 0.44) and grains per panicle (P = 0.40) via panicle weight implying that these traits may be used to indirectly select for higher yields. Of these traits, a thousand grain weight had high narrow sense heritability (82%) indicating that improvement on grain yield may begin in early generation by indirectly selecting for higher a thousand grain weight via heavy panicle weight. This is because although a thousand grain weight was negatively correlated with grain yield it had a positive and significant association with panicle weight.

6.5 Conclusion

In conclusion, high levels of narrow sense heritability estimates were observed for days to heading, days to anthesis and days to maturity suggesting that simple recurrent selection may be employed to enhance development of drought escaping cultivars adapted to the rainfed upland and lowland ecosystems in coastal lowlands of Kenya. In addition, the narrow sense heritability estimates were high for a thousand grain weight indicating that this too may be improved through simple recurrent selection. In contrast, narrow sense heritability estimates were low for grain yield and the other yield components; spikelet fertility, number of grains per panicle, panicle weight and weight of grains per panicle suggesting that hybridization can be a choice for developing hybrids with high yield and desirable traits of the other yield components. It also suggests that selection based on these traits would not be effective in early generations but in the later generations.

Path analysis coefficients and forward multiple regression analysis results were in agreement that number of productive tillers per plant, panicle weight and spikelet fertility, were important direct contributors to yield improvement. Thus these traits may be used for direct selection of grain yield. However, the heritability estimates were moderate for number of productive tillers per plant and low for panicle weight and spikelet fertility suggesting that these traits may be utilized for pure line selection in late generations. Although positive and indirect effects on grain yield were observed for weight of grains per panicle, a thousand grain weight and grains per panicle via panicle weight, a thousand grain weight may be the trait of choice because it exhibited high narrow sense heritability indicating that yield improvement may begin in early generation by indirectly selecting for a higher thousand grain weight via heavy panicle weight. Moreover, a thousand grain weight had a positive and significant association with panicle weight though it showed a negative association with grain yield.

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Chapter Seven

Genotype × environment interactions for grain yield in rice under no drought and drought conditions

Abstract

Environments in sub-Saharan Africa fluctuate considerably across sites and seasons. This suggests the importance of assessing genotype x environment interaction (GEI) in cultivar development. The objective of this study was to a) estimate the magnitude of genotype x environment interaction for grain yield; b) identify high yielding and stable genotypes across the test environments; and c) identify the most discriminating and representative environments as future mutli-locational rice testing sites in the coastal region of Kenya. Ten rice pure lines consisting of five interspecific and five O*ryza sativa* L. lines were mated in half- diallel mating design and F_1's advanced to F_3 generation. Fifty six genotypes including 45 F_3 populations, their 10 parents and one check were evaluated in 7 x 8 alpha lattice design with two replications under three no drought and one random managed drought stress condition at reproductive growth stage at three sites in coastal region of Kenya. The additive main effects and multiplicative interaction (AMMI) analysis and genotype plus genotype x environment interaction (GGE) biplot analysis were used to measure grain yield stability of the 45 F_3 populations and their 10 parents. The genotype and environment main effects and their interactions were highly significant ($P < 0.001$). Ranking of the genotypes changed across environments revealing a crossover type of GEI. The four environments fell into three mega environments. The AMMI and GGE biplot analysis identified G37 (Luyin 46 x IR55423-01) as the highest yielding genotype across environments. Based on GGE biplot results, G39 and G40 combined high yield and stability across the test environments and therefore good for general adaptation. Genotypes that showed specific adaptation were G37 for Matuga and, G38 and G41 for Msambweni no drought condition. Msambweni random managed drought condition was positively correlated to Mtwapa and Matuga upland ecologies and was the most discriminating and representative of the test environments. Therefore, the site may be good for selecting genotypes with general adaptation for the upland ecology and drought tolerant genotypes for the lowland ecology.

Keywords: Additive main effects and multiplicative interaction (AMMI), genotype x environment interactions, genotype plus genotype x environment interaction (GGE) biplot, rice, yield stability

7.1 Introduction

Genotype x environment interaction (GEI) is the differential genotypic responses to environmental changes (Baker, 1988, Crossa, 1990, Romagosa and Fox, 1993). The genotypic main effects provide adequate information about the performance of the genotypes across environments in the absence of GEI. However, with significant GEI, differences between genotypes vary widely among environments (Annicchiarico, 2002). A significant GEI, is manifested either as changes in the absolute differences between the genotypes without affecting the rank order (non-crossover) or as rank order changes of the genotypes between environments (crossover GEI) (Crossa *et al.*, 1995; Yan and Hunt, 2001; Bernardo, 2002). The crossover type of GEI is the most important to plant breeders (Fox *et al.*, 1997). It reduces the association between phenotypic and genotypic values complicating selection of superior cultivars and best testing sites for identifying superior and stable genotypes (Flores *et al.*, 1998). Consequently, progress in providing farmers with high yielding cultivars is slowed down (Ceccarelli *et al.*, 2006).

With occurrence of a large GEI, plant breeders tend to identify and recommend high yielding and stable genotypes that show little interaction with the environment or genotypes specifically adapted to certain environments (Annicchiarico, 2002; Fan *et al.*, 2007). Several statistical methods which include regression (Finlay and Wilkison, 1963; Eberhart and Russell, 1966), principal component analysis (PCA) (Hill and Goodchild, 1981), additive main effects and multiplicative interaction (AMMI) (Gauch and Zobel, 1988) and genotype plus genotype by environment (GGE) analysis (Yan, 2001) have been developed to assess stability of a set of genotypes and patterns of GE. Of these, AMMI and GGE biplot are widely used. The AMMI model combines analysis of variance with PCA analysis generating a family of models (Yan and Hunt, 2001; Carlos *et al.*, 2003). However, it is only the AMMI1 and AMMI2 models that may be used to visualise GEI patterns (Yan and Hunt, 2001). In AMMI1 a biplot of main effects with interaction PCA1 (IPCA1) facilitates visualisation of correlation among environments and the response patterns of the genotypes and their interactions with the environments by using sign and magnitude of IPCA1 values (Yan and Hunt, 2001). In AMMI2 a biplot of IPCA1 and IPCA2 is constructed which visualises magnitude of interaction for each genotype and environment (Yan and Hunt, 2001).

The GGE biplot analysis on the other hand puts together genotypic main effects (G) and genotype x environment interaction (GE) to facilitate graphical visualisation of cultivar evaluation and mega environment identification (Yan *et al.*, 2000; Yan, 2002). The GGE biplot is constructed by the first two symmetrically scaled principal components (PC1 and

PC2) derived from singular value decomposition (SVD) of environment centred data (Yan *et al.*, 2000; Yan, 2002). This biplot is useful in visualisation and identification of the mega environments, specific and wide cultivar adaptations, high yielding and stable cultivars and interrelationship among environments (Yan, 2001).

In sub-Saharan Africa, significant GEI for grain yield and other agronomic traits has clearly been demonstrated in studies involving evaluation of major field crops of economic importance (Badu-Apraku *et al.*, 2011a; 2011b; Sanni *et al.*, 2012; Nassir, 2013). For example, in a study involving rice germplasm evaluated in five environments in south West Africa, the AMMI analysis revealed significant GEI for grain yield and panicle attributes (Nassir, 2013). On grain yield, the first PCA axis of the interaction captured 52% of the interaction sum of squares while the GGE biplot captured 64% of the interaction component (Nassir, 2013). In another study evaluating 22 NERICA cultivars in three environments in two years again in West Africa the AMMI analysis reported the existence of a significant GEI with the first four IPCA's contributing 98.5% of the total interaction sum of squares (Sanni *et al.*, 2009). Significant GEI estimated using AMMI and GGE biplot statistical methods has also been reported in studies involving multi-location trials of maize germplasm across years in West Africa (Badu-Apraku *et al.*, 2011a; 2011b) and in east Africa (Beyene *et al.*, 2012). These studies clearly indicate that in sub-Saharan Africa, environmental conditions fluctuate considerably across years and locations and suggest the importance of considering GE effects in cultivar development and release.

At the beginning of this decade a rice breeding programme was started at the Kenya Agricultural and Livestock Research Institute (KALRO) - Mtwapa to develop high yielding drought tolerant rice cultivars for the lowland and upland rice ecologies in the coastal lowlands of Kenya. Selected interspecific and *Oryza sativa* L. pure lines were hybridized and the breeding materials advanced to the third generation (F_3). At this stage, there is need to identify and select promising populations so as to reduce the numbers to manageable levels. The objective of this study was therefore to a) estimate the magnitude of GEI for grain yield; b) identify high yielding and stable genotypes across the test environments and c) identify the most discriminating and representative environments as future multi-locational rice testing sites in the coastal lowlands of Kenya. This study is not meant for cultivar recommendation *per se* but to undertake early generation selections in F_3 populations.

7.2 Materials and methods

7.2.1 Germplasm

Fifty five genotypes which included 45 F_3 populations obtained from 10 x 10 half diallel mating design described in chapter 4 section 4.2.4 and their 10 parents described in chapter 4 Table 4.2.2, were used in this study. The codes and pedigree of the parental genotypes and their crosses are given in Table 7.1 and 7.2, respectively.

Table 7.1: Code and variety name/pedigrees of the 10 parental genotypes used in the diallel

Code	**Variety name/Pedigree**	**Species**
P1	NERICA 1	Interspecific
P2	NERICA 2	Interspecific
P3	*Duorado* precoce	*Oryza Sativa*
P4	CT16333(1)-CA-22-M	Interspecific
P5	CT16323-CA-25-M	Interspecific
P6	Luyin 46	*Oryza Sativa*
P7	NERICA -L- 25	Interspecific
P8	IR55423-01	*Oryza Sativa*
P9	Vandana	*Oryza Sativa*
P10	IR74371-54-1-1	*Oryza Sativa*

7.2.2 Environments

Grain yield of the 55 entries was evaluated in four environments; three environments represented no drought conditions under upland and lowland ecology and one random managed drought conditions under lowland ecology. Features of the four environments are summarised in Table 7.3 and described in details in chapter 4, Section 4.2.1.

Table 7.2: Codes and pedigrees for the 45 F_3 rice populations obtained from 10 x 10 half diallel mating design.

45 F_3 rice populations					
Code	Pedigree	Code	Pedigree	Code	Pedigree
G1	NERICA 1 x NERICA 2	**G16**	NERICA 2 x Vandana	**G31**	CT16323-CA-25-M x Luyin 46
G2	NERICA 1 x *Duorado*	**G17**	NERICA 2 x IR74371-54-1-1	**G32**	CT16323-CA-25-M x NERICA-L-25
G3	NERICA 1 x CT16333(1)-CA-22-M	**G18**	*Duorado* x CT16333(1)-CA-22-M	**G33**	CT16323-CA-25-M x IR55423-01
G4	NERICA 1 x CT16323-CA-25-M	**G19**	*Duorado* x CT16323-CA-25-M	**G34**	CT16323-CA-25-M x Vandana
G5	NERICA 1 x Luyin 46	**G20**	*Duorado* x Luyin 46	**G35**	CT16323-CA-25-M x IR74371-54-1-1
G6	NERICA 1 x NERICA-L-25	**G21**	*Duorado* x NERICA-L-25	**G36**	Luyin 46 x NERICA-L-25
G7	NERICA 1 x IR55423-01	**G22**	*Duorado* x IR55423-01	**G37**	Luyin 46 x IR55423-01
G8	NERICA 1 x Vandana	**G23**	*Duorado* x Vandana	**G38**	Luyin 46 x Vandana
G9	NERICA 1 x IR74371-54-1-1	**G24**	*Duorado* x IR74371-54-1-1	**G39**	Luyin 46 x IR74371-54-1-1
G10	NERICA 2 x *Duorado*	**G25**	CT16333(1)-CA-22-M x CT16323-CA-25-M	**G40**	NERICA-L-25 x IR55423-01
G11	NERICA 2 x CT16333(1)-CA-22-M	**G26**	CT16333(1)-CA-22-M x Luyin 46	**G41**	NERICA-L-25 xVandana
G12	NERICA 2 x CT16323-CA-25-M	**G27**	CT16333(1)-CA-22-M x NERICA-L-25	**G42**	NERICA-L-25 x IR74371-54-1-1
G13	NERICA 2 x Luyin 46	**G28**	CT16333(1)-CA-22-M x IR55423-01	**G43**	IR55423-01 x Vandana
G14	NERICA 2 x NERICA-L-25	**G29**	CT16333(1)-CA-22-M x Vandana	**G44**	IR55423-01 x IR74371-54-1-1
G15	NERICA 2 x IR55423-01	**G30**	CT16333(1)-CA-22-M x IR74371-54-1-1	**G45**	Vandana x IR74371-54-1-1

Table 7.3: Features of the four environments used in this study

Study site	Zonation	Season	Type of Environment	Mean annual Rainfall (mm)	Altitude (m)
Matuga	Coastal lowland 3 (CL3)	Short rain season (2014/15)	No drought stress	1200	132
Mtwapa	Coastal lowland 3 (CL3)	Short rain season (2014/15)	No drought stress	1200	15
Msambweni	Coastal lowland 2 (CL2)	Short rain season (2014/15)	Random drought stress	1400	19
Msambweni	Coastal lowland 2 CL2)	Long rain season (2015)	No drought stress	1400	19

7.2.3 Experimental design and management of trials

The 55 entries and one check (not used in the analysis because it was late maturing) were laid out in 7 x 8 alpha lattice designs with two replications. Management of experiments is described in chapter 4 section 4.2.2 to 4.2.6

7.2.4 Data collection

Grain yield data was taken as the weight of unhulled grains harvested from an area of 2 m^2 for the experiments planted under field conditions and from 40 plants for the experiment planted in pots. This was then converted to tons ha^{-1} at 14% moisture content.

7.2.5 Data analysis

A combined analysis of variance (ANOVA) was performed to determine the effects of environment, genotype and GEI on grain yield of the 45 F_3 populations and their 10 parents across four environments using PROC GLM in SAS (SAS Institute, 2012). The Genstat statistical package (14th Edition) (Payne *et al.*, 2011) was used to estimate and graphically visualise grain yield stability of the 45 F_3 populations using the AMMI (Additive Main Effects and Multiplicative Interaction) and the GGE (genotype and genotype x environment) biplot analyses.

The AMMI analyses were performed to clarify the presence of the GEI, summarize patterns and relationships of genotypes and environments and estimate the grain yield means that are adjusted for G x E using the model shown below (Crossa, 1990).

$$Y_{ij} = \mu + g_i + e_j + \sum_{k=1}^{t} \lambda_k \xi_{ik} \eta_{jk} + \varepsilon_{ij}$$

Where, Y_{ij} is the mean yield (t ha^{-1}) of the ith genotype in the jthenvironment, μ is the overall mean, g_i and e_j are the main effects of the genotype and environment respectively, t is the number of PCA axes considered, k is the singular value of kth PCA axis, λ_k Eigenvalues for kth PCA axis, ξ_{ik} and η_{jk} are scores for the ith genotype and jth environment on the kth PCA axis, and ε_{ij} is the residual term which includes experimental error

The AMMI biplot showing the main effects (genotype and environment) and the first interaction principal components axis (IPCA 1) was also presented to assess the relationships among crosses, test environments and GEI for grain yield.

The GGE mathematical model based on PCA of environment-centred data (which contains G and GE as the main sources of variation) subjected to singular value decomposition (SVD) was used to visualize the relationship among genotypes and the environments. The basic model for a GGE biplot as described by Yan (2002) is:

$$Y_{ij} - \mu - \beta_j = \sum_{l=1}^{k} \lambda_l \, \xi_{il} \eta_{lj} + \varepsilon_{ij}$$

Where:-

Y_{ij} = Mean grain yield (t ha^{-1}) of the ith genotype in the jth environment; μ = Overall mean; β_j = main effect of the environment; λ_l = eigen value associated with IPCA l; ξ_{il} = the eigenvector of genotype *i* for PC l; η_{lj} = the eigenvector of environment *j* for PC l; ε_{ij} = error term associated with rice genotype *i* in environment *j*.

GGE biplot graphs were used to visualize interrelationships among the test environments, discriminating ability and representativeness of test environments, which-won-where-pattern polygon view and mean yield and stability among genotypes (Yan and Tinker, 2006; Yan *et al.*, 2007). In the biplot of interrelationships among the test environments, vectors are drawn from the biplot origin to each marker of the environment to facilitate visualization of relationships among environments. The cosine of the angle between the environment vectors approximates correlation between any two environments. Acute angles indicate a positive correlation; obtuse angles indicate a negative correlation and right angles no correlation (Yan and Tinker, 2006)

Environment ranking based on both discriminating ability and representativeness view of GGE biplot displays a single arrowed line known as Average-Environment Coordinate (AEC) abscissa that passes through the biplot origin and the average environment of all the test environments. The arrow points towards the average environment. Concentric circles to help visualize the distance between the test environments and the average environment are drawn with the center at the end of the arrow head representing the average environment. The projection of the average environment on the AEC abscissa from the center of the biplot is equal to the longest vector of all the test environments and therefore the most discriminating; its projection on the AEC ordinate is zero and therefore the most representative. Test environments closer to the average environment are most discriminating and representative and therefore the best for selecting cultivars with general adaptations. In contrast, test environments further away from the average environment are the worst for selecting genotypes adapted to the whole region (Yan, 2001; Yan and Tinker, 2006; Yan *et al.*, 2007).

The which-won-where GGE biplot consist of an irregular polygon drawn on genotypes that are furthest from the biplot origin so that all other genotypes are contained within the polygon. Perpendicular lines that start form the biplot origin divide the polygon into sectors representing hypothetical environments. Each sector has its own winning genotype which is the vertex genotype at the intersection of the two polygon sides whose perpendicular lines form the boundary of that sector. The environmental markers may fall into a single sector indicating non crossover type of GE or into different sectors indicating crossover type of GE (Yan and Tinker, 2006; Yan *et al.*, 2007)

The mean performance and stability of the genotypes GGE biplot is used to compare genotypes based on their mean performance and stability across environments within a mega environment. The genotypes are graphically plotted on a biplot defined by two lines; the AEC abscissa and the AEC ordinate. The AEC abscissa is a single arrowed line that passes through the biplot origin and the average environment pointing to higher mean yield across environments and hence ranks the genotypes with respect to mean performance. The AEC ordinate is a double arrowed line passing through the biplot origin and perpendicular to the AEC abscissa. It indicates the variability of the genotypes and points to poorer variability in either direction. Lines connecting each individual genotype from the AEC abscissa and parallel to the AEC ordinate are used to visualize stability of each genotype.

Genotypes located on the AEC abscissa line are the most stable while those further away are the most unstable (Yan and Tinker, 2006; Yan *et al.*, 2007).

7.3 Results

7.3.1 Analysis of variance and AMMI analysis

The combined analysis of variance for grain yield showed highly significant ($P<0.001$) genotype (G), environment (E) and genotype × environment (G×E) interaction explaining 25, 6 and 53% of the total sum of squares respectively (Table 7.4). The G×E interaction effect was approximately nine times that of environmental effect and twice that of the genotype effect. The AMMI analysis of variance showed that grain yield of 55 genotypes at four environments was significantly ($P \leq 0.001$) affected by the genotype, environment and genotype x environment interaction explaining 30, 7 and 63% of the total treatment sum of squares, respectively. The first and the second PCA axis (IPCA1 and IPCA2) of the interaction were highly significant ($P<0.001$). The IPCA1 explained 31% of the treatment sum of squares which is 48% of the G x E interaction sum of squares in 35% of the interaction degrees of freedom. The IPCA2 explained 17% of the treatment sum of squares which is 27% of the G x E interaction sum of squares in the remaining 33% of the interaction degrees of freedom.

7.3.2 Ranking of the best four AMMI selections per environment

The AMMI average genotype grain yield ranged from 4.53 t ha^{-1} in G37 to 2.28 t ha^{-1} in G28 (Table 7.5). Grain yield for environments was highest at Msambweni under no drought conditions (3.7 t ha^{-1}) and lowest at Msambweni – random drought conditions (3.0 t ha^{-1}). Differential ranking was observed among the 55 genotypes for grain yield across the four test environments (Table 7.6). The best genotypes under no drought conditions in each environment were G45 (Vandana x IR74371-54-1-1) in Matuga, G1 (NERICA 1 x NERICA 2) in Mtwapa and G38 (Luyin 46 x Vandana) in Msambweni while G39 (Luyin 46 x IR74371-54-1-1) was the best genotype in Msambweni under drought conditions. Genotypes that showed good performance in more than one environment were genotype G37 (Luyin 46 x IR55423-01) as the second best in Mtwapa and third best in Msambweni no drought condition and genotype G42 (NERICA-L-25 x IR74371-54-1-1) as second best in Msambweni drought conditions and fourth best in Mtwapa.

Table 7.4: ANOVA of grain yield (t ha^{-1}) of 55 rice genotypes (45 F_3 populations and 10 parents) across one random drought and three no drought environments

Source of variation	**DF**	**SS**	**MS**	**%total SS explained**	**Prob**
REP(ENV)	3	2.07	0.69		0.1114
Environment (E)	3	25.74	8.58	5.73	<.0001
Genotype (G)	54	112.15	2.08	24.95	<.0001
Interactions (G x E)	162	235.90	1.46	52.49	<.0001
Error	216	73.47	0.34	16.35	
Total	439	449.43			

Table 7.5: AMMI analysis of variance for grain yield (t ha^{-1}) of 55 rice genotypes (45 F_3 populations and 10 parents) across one random drought and three no drought environments

Source of variation	**DF**	**SS**	**MS**	**F**	**% Total SS explained**	**% Treatment SS explained**	**% G X E interaction SS explained**	**Prob**
Block	4	2.20	0.54	1.60				0.175
Treatments	219	374.20	1.71	5.02	83.19			<.000
Genotype (G)	54	112.30	2.08	6.11		30.01		<.000
Environments (E)	3	25.80	8.60	15.81		6.89		<.001
Interactions (G x E)	162	236.10	1.46	4.28		63.09		<.000
IPCA 1	56	114.10	2.04	5.99		(30.49)	48.33	<.000
IPCA 2	54	63.80	1.18	3.48		(17.05)	27.02	<.000
Residuals	52	58.20	1.12	3.29				
Error	216	73.50	0.34		16.34			
Total	439	449.80	1.03					

Table 7.6: The best four genotypes from AMMI analysis at each environment

Environment	Mean GY (t ha^{-1})	PCA Score	Rank			
			1	2	3	4
Msambweni (DRT)	3.00	1.28	G39†	G42	G55	G2
Mtwapa	3.24	0.55	G1	G37	G34	G42
Matuga	3.39	0.48	G45	G10	G18	G53
Msambweni	3.67	-2.32	G38	G41	G37	G51

† Pedigree and codes of the genotypes are given in Table 7.2

Table 7.7: AMMI average grain yield (t ha^{-1}) of 45 F_3 rice populations and their 10 parents evaluated under three no drought and one random managed drought stress condition at three sites in coastal lowlands of Kenya..

Code	**Genotypes**	**Environments**				**Mean**
		Matuga	**Mtwapa**	**Msambweni**	**Msambweni**	
		No Drought			**Drought**	
G1	NERICA 1 x NERICA 2	4.43	4.19	3.94	4.05	4.15
G2	NERICA 1 x *Duorado*	3.13	3.73	3.19	4.20	3.56
G3	NERICA 1 x CT16333(1)-CA-22-M	4.17	3.49	3.10	3.11	3.47
G4	NERICA 1 x CT16323-CA-25-M	3.82	3.31	2.60	3.12	3.22
G5	NERICA 1 x Luyin 46	2.84	2.31	3.19	1.73	2.52
G6	NERICA 1 x NERICA -L- 25	3.45	2.91	3.86	2.31	3.13
G7	NERICA 1 x IR55423-01	3.38	3.32	2.41	3.47	3.15
G8	NERICA 1 x Vandana	3.77	2.99	4.84	2.02	3.40
G9	NERICA 1 x IR74371-54-1-1	2.28	3.10	4.00	3.36	3.18
G10	NERICA 2 x *Duorado*	5.12	3.38	3.22	2.29	3.50
G11	NERICA 2 x CT16333(1)-CA-22-M	3.47	3.94	4.09	4.15	3.91
G12	NERICA 2 x CT16323-CA-25-M	3.19	2.63	3.57	2.02	2.85
G13	NERICA 2 x Luyin 46	3.07	3.07	4.84	2.60	3.39
G14	NERICA 2 x NERICA -L- 25	2.15	3.31	4.47	3.72	3.41
G15	NERICA 2 x IR55423-01	3.56	3.38	3.66	3.16	3.44
G16	NERICA 2 x Vandana	3.11	2.86	4.13	2.36	3.12
G17	NERICA 2 x IR74371-54-1-1	2.99	2.82	3.22	2.57	2.90
G18	*Duorado* x CT16333(1)-CA-22-M	4.89	3.64	2.07	3.20	3.45
G19	*Duorado* x CT16323-CA-25-M	3.82	3.59	2.39	3.69	3.37
G20	*Duorado* x Luyin 46	2.49	2.67	3.48	2.55	2.80
G21	*Duorado* x NERICA -L- 25	2.57	2.75	2.83	2.81	2.74
G22	*Duorado* x IR55423-01	3.06	2.23	2.53	1.60	2.35
G23	*Duorado* x Vandana	3.12	2.72	2.81	2.40	2.76
G24	*Duorado* x IR74371-54-1-1	2.62	2.58	2.45	2.55	2.55
G25	CT16333(1)-CA-22-M x CT16323-CA-25-M	3.85	3.08	2.64	2.66	3.06

G26	CT16333(1)-CA-22-M x Luyin 46	2.63	2.45	2.79	2.21	2.52
G27	CT16333(1)-CA-22-M x NERICA -L- 25	2.55	3.14	2.30	3.68	2.92
G28	CT16333(1)-CA-22-M x IR55423-01	2.62	1.96	3.38	1.15	2.28
G29	CT16333(1)-CA-22-M x Vandana	3.04	2.82	3.38	2.51	2.94
G30	CT16333(1)-CA-22-M x IR74371-54-1-1	3.81	3.03	3.30	2.44	3.14
G31	CT16323-CA-25-M x Luyin 46	2.56	2.57	3.35	2.34	2.70
G32	CT16323-CA-25-M x NERICA -L- 25	2.20	3.19	2.94	3.84	3.04
G33	CT16323-CA-25-M x IR55423-01	2.90	2.85	2.56	2.84	2.79
G34	CT16323-CA-25-M x Vandana	4.24	3.96	4.12	3.71	4.01
G35	CT16323-CA-25-M x IR74371-54-1-1	3.03	2.86	3.01	2.68	2.90
G36	Luyin 46 x NERICA -L- 25	2.54	3.10	5.33	2.88	3.46
G37	Luyin 46 x IR55423-01	3.96	4.15	6.31	3.70	4.53
G38	Luyin 46 x Vandana	4.35	3.56	6.75	2.24	4.23
G39	Luyin 46 x IR74371-54-1-1	2.05	3.77	4.65	4.61	3.77
G40	NERICA -L- 25 x IR55423-01	3.90	3.89	4.27	3.75	3.95
G41	NERICA -L- 25 x Vandana	4.06	3.78	6.40	2.93	4.29
G42	NERICA -L- 25 x IR74371-54-1-1	3.38	3.94	3.56	4.35	3.81
G43	IR55423-01 x Vandana	3.43	3.83	3.87	4.03	3.79
G44	IR55423-01 x IR74371-54-1-1	3.21	3.73	3.43	4.10	3.62
G45	Vandana x IR74371-54-1-1	5.17	3.82	3.70	2.97	3.91
Parents						
P1	NERICA 1	3.84	3.50	3.60	3.23	3.54
P2	NERICA 2	3.55	3.48	3.60	3.36	3.50
P3	*Duorado* precoce	3.64	3.84	3.65	3.97	3.77
P4	CT16333(1)-CA-22-M	3.94	3.14	3.10	2.60	3.20
P5	CT16323-CA-25-M	3.80	3.38	2.25	3.35	3.20
P6	LUYIN 46	2.49	3.13	6.09	2.78	3.62
P7	NERICA -L- 25	3.06	2.38	5.26	1.22	2.98
P8	IR55423-01	4.71	3.43	3.76	2.51	3.60
P9	Vandana	4.31	3.62	4.74	2.86	3.88
P10	IR74371-54-1-1	2.89	3.62	2.60	4.30	3.35
Mean		**3.39**	**3.24**	**3.67**	**3.00**	**3.32**

7.3.3 AMMI GE and IPCA scores biplot

The complete AMMI (combined main effects and IPCA1) explained 67% of the total treatment variation while AMMI2 (IPCA 1+IPCA 2) explained 48% of the total treatment variation. AMMI2 was dropped in favour of AMMI1. This is because the noise in the treatment sum of squares in AMMI1 was less, 31%, compared to 48% in AMMI2. Thus AMMI1 was more effective because it had less predictive errors. Therefore a biplot of main effects against IPCA1 was used to graphically visualise average productivity of the genotypes and environments and GE interaction for all possible genotype x environment combinations. The four environments fell into three groups: Matuga had large positive

IPCA1 score strongly interacting positively with genotypes that had positive IPCA scores and negatively with genotypes that had negative IPCA scores (Figure 7.1). Msambweni drought condition had large negative IPCA1 score strongly interacting with genotypes but in the opposite direction to that of Matuga. Mtwapa and Msambweni no drought condition formed the third group with small IPCA1 scores suggesting that they had little interaction with the genotypes. The genotypes showed variability in mean yield and in interaction scores. Genotype G37 was the highest yielding followed by G41, G38, G1 and G34. The most stable high yielding genotypes were G41, G1 and G34 in that rank order. The most unstable but high yielding genotypes demonstrating a strong GEI were G10 and G39. G10 was specifically suitable for Matuga while G39 was suitable for Msambweni no drought condition.

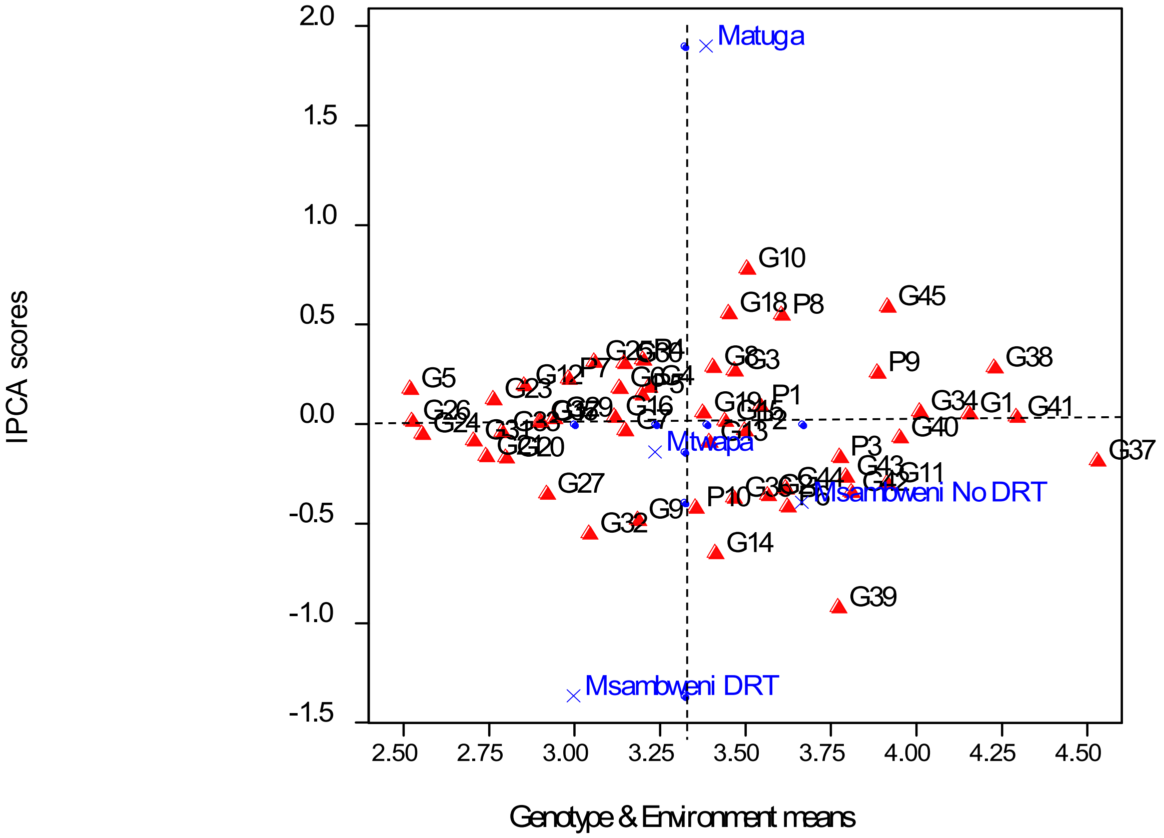

Figure 7.1: AMMI1 biplot of grain yield of 45 F_3 rice populations (G1-G45) and their parents (P1 – P10) across four environments. See Tables 7.1 and 7.2 for genotype codes and pedigrees

7.3.4 GGE biplot analysis

7.3.4.1 Relationship among test environments

The goodness of fit of the GGE biplot was 67.94%; PC1 contributed 39.01% while PC2 accounted for 28.93% of the total variation (Figure 7.2). The cosine of the angle between vectors of Msambweni no drought and drought condition was a right angle. The acute angle between vectors of Msambweni drought condition and Mtwapa was the smallest and largest between vectors of Mtwapa and Msambweni no drought condition. The distance between Msambweni drought condition and Mtwapa was the smallest followed by the distance between Mtwapa and Matuga. The distance between Mtwapa and Matuga from Msambweni drought environment was shorter than the distance between these two sites from Msambweni no drought environment.

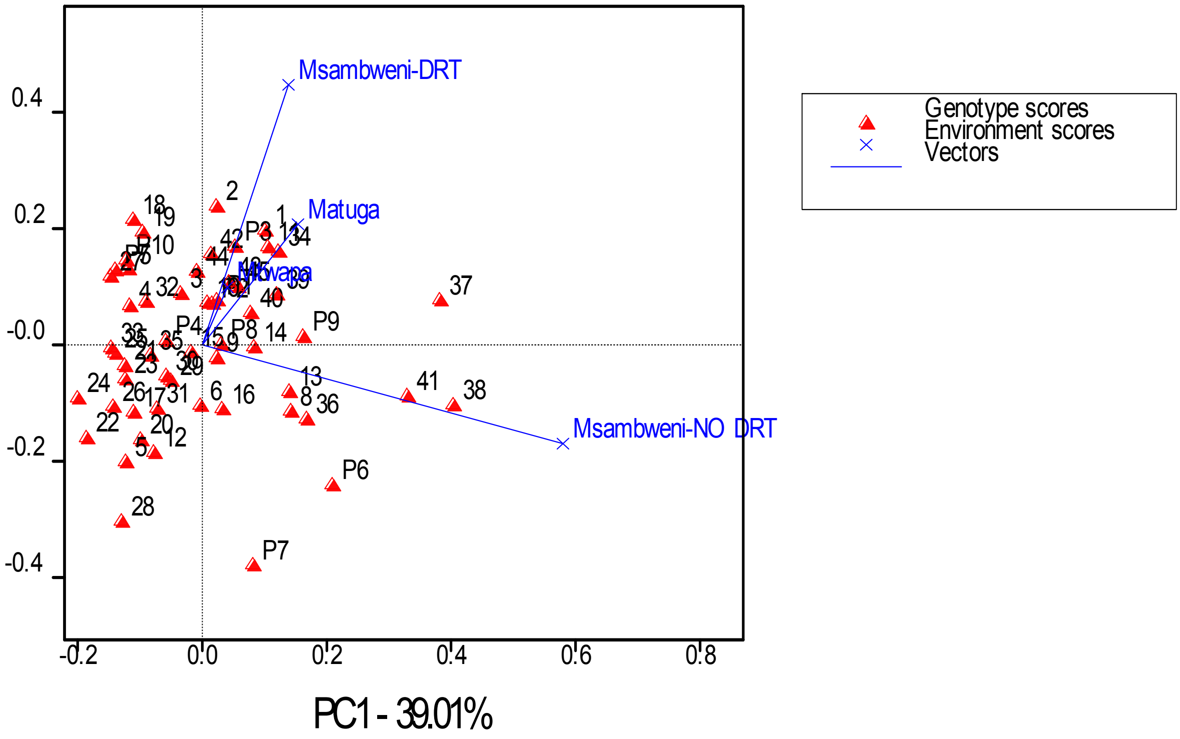

Figure 7.2: Relationship among test environments. See Tables 7.1 and 7.2 for genotype codes and pedigrees

7.3.4.2 Environment ranking based on discriminating ability and representativeness

Environments were ranked based on discriminating ability and representativeness of the 'ideal" (average) environment (Figure 7.3). Matuga and Msambweni drought were found to be close to the average environment and therefore the most representative of the target region. However, Msambweni drought had a longer vector than Matuga and therefore was both discriminating and representative of the whole region. Msambweni no drought and Mtwapa were further away from the average environment and therefore the least representative of the whole region. Msambweni drought had a long vector and therefore classified as discriminating and non-representative. Mtwapa was both non-discriminating and non-representative of the target region since it had a short vector and was further away from the average environment.

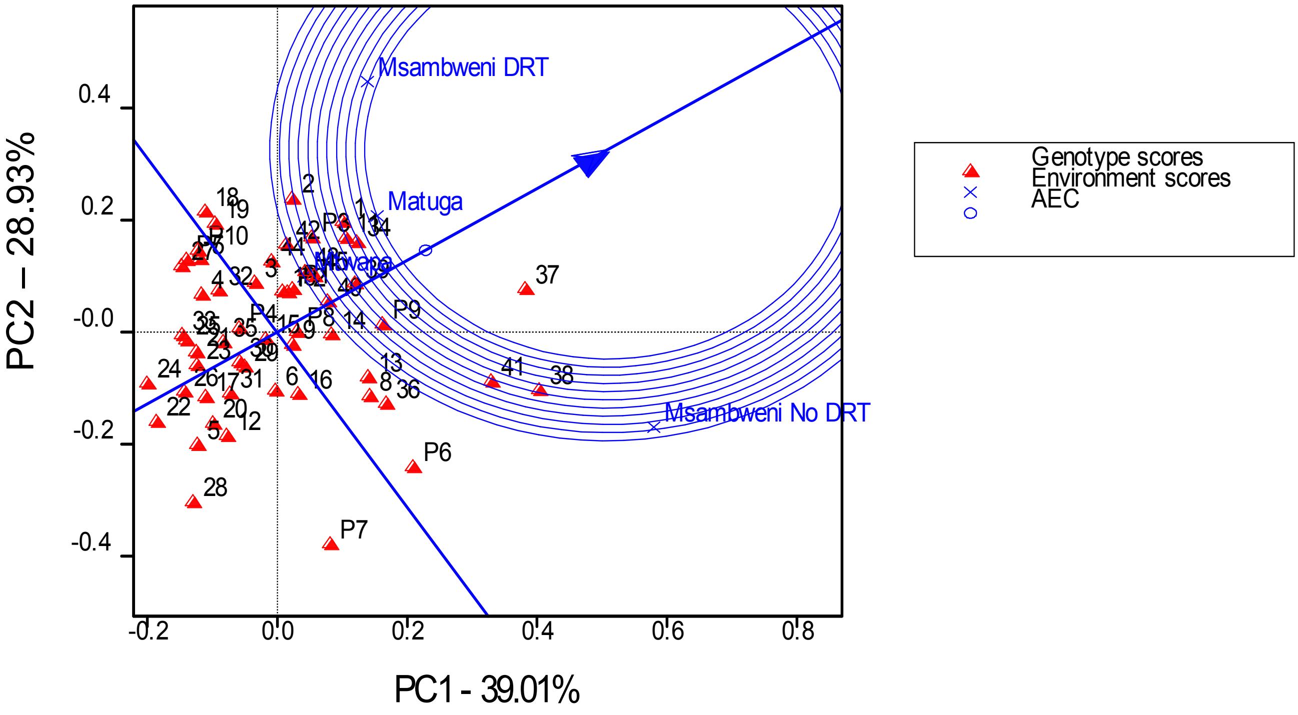

Figure 7.3: The discriminating and representative view showing the discriminating ability and representativeness of the test environments. See Tables 7.1 and 7.2 for genotype codes and pedigrees

7.3.4.3 The Which-Won-Where polygon view

The polygon view of the GGE biplot displayed which won where pattern of genotype by environment dataset of the three no drought and one drought environment (Figure 7.4). The radial lines originating from the centre of the biplot divided the polygon into eight sectors.

The four environments fell into three sectors and there were three mega environments. The first mega environment consisted of Mtwapa and Msambweni drought condition and the winning genotype was G2. The second mega environment was represented by Matuga and the winning genotype was G37. The third was represented by Msambweni no drought condition and here the winning genotype was G38.

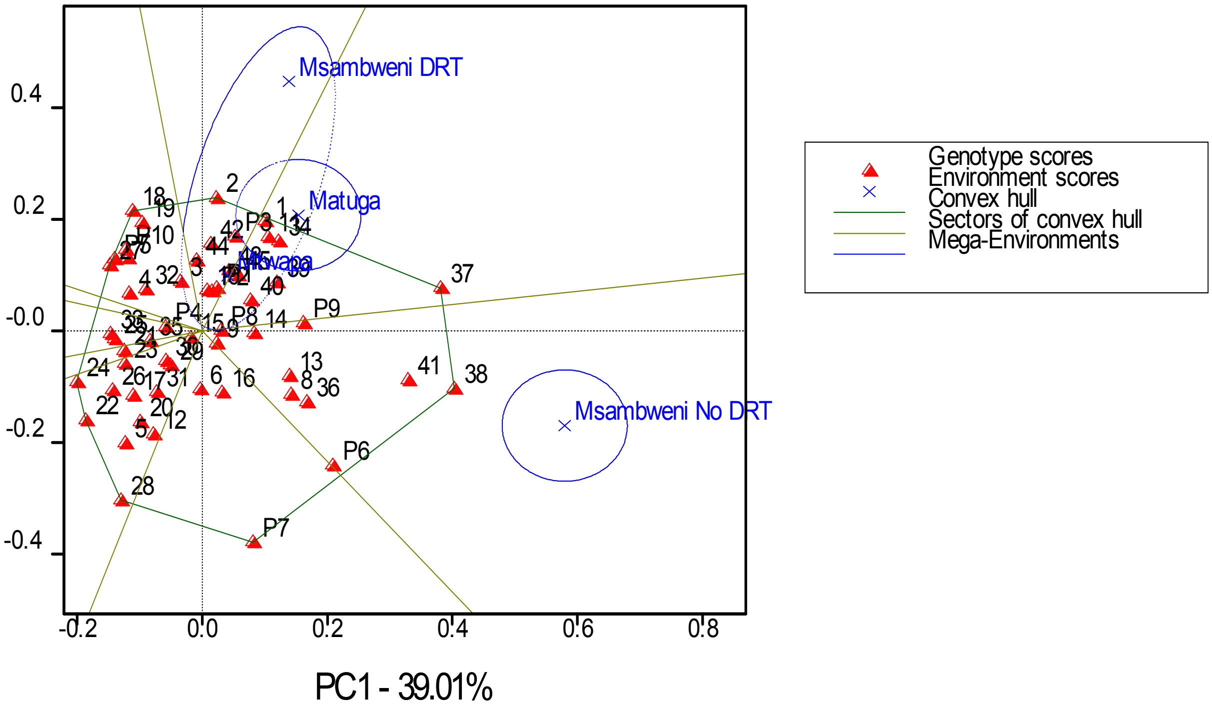

Figure 7.4: Polygon view of the GGE biplot based on symmetrical scaling. See Tables 7.1 and 7.2 for genotype codes and pedigrees

7.3.4.4 Mean yield and stability of genotypes

Among the F_3 populations, genotype G37 had the highest grain yield followed by G38 and G41 in that rank order (Figure 7.5). Genotype G28 was the lowest yielding genotype. Among the parents P9 was the highest yielding parent followed by P3, P6 and P8. The lowest yielding parent was P7. Grain yield of seven F_3 populations namely G37, G38, G41, G1, G34, G11, G2 and G39, was higher than the highest yielding parent P9. The most stable F_3 population with above average mean performance was G39 as it was located almost on the AEC abscissa and had a near zero projection onto the AEC ordinate. This was followed by G40. In contrast, G38 although high yielding, was the least stable followed by G41. Parent P8 (close to G14) was found to be the most stable parent although it was located slightly away from the AEC abscissa. Parents P6 and P7 were found to be the most unstable among parents with almost similar level of poor stability with G41

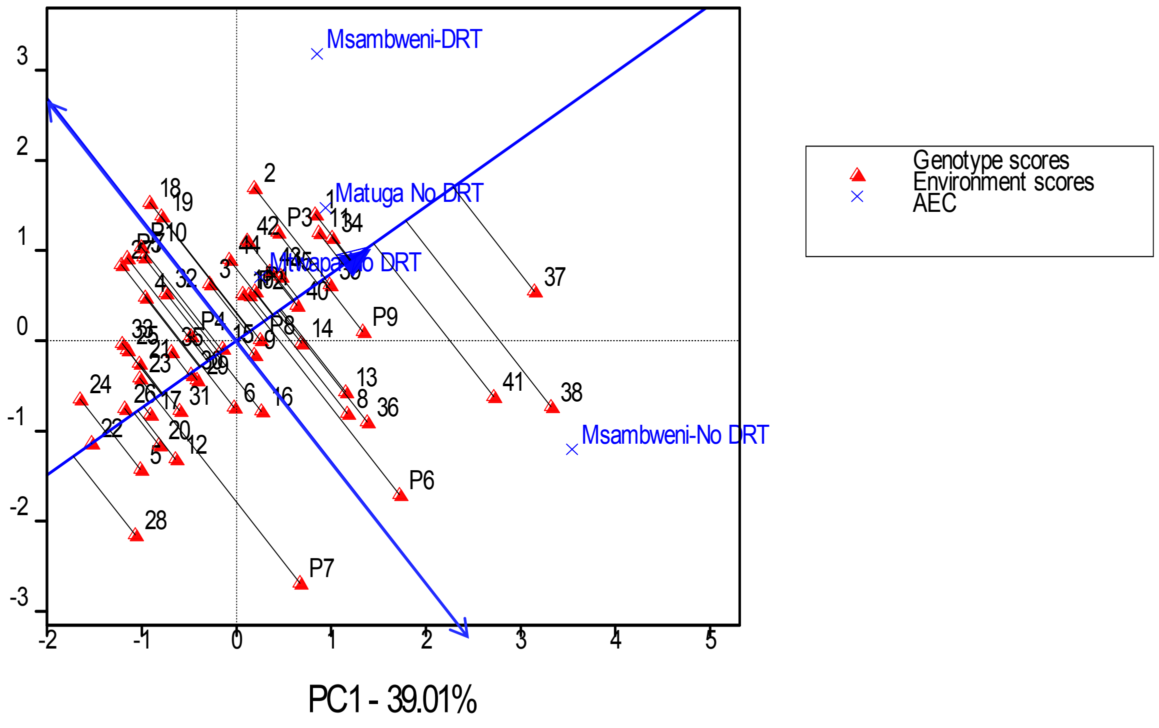

Figure 7.5: GGE-biplot based on genotype-focused singular value partitioning for comparison of the genotypes with the ideal genotype. See Tables 7.1 and 7.2 for genotype codes and pedigrees

7.4 Discussion

7.4.1 ANOVA and AMMI analysis

The ANOVA and AMMI analysis revealed that the environment and genotypic main effects and their interactions were highly variable. The genotype x environment interaction (GEI) for grain yield contributed approximately 50% of the total sum of squares. These effects were greater than what has been obtained in other studies (Sanni *et al.*, 2009; Nassir, 2013). The high interaction effects observed could partly be explained by the wide variation between the genotypes and among the environments. The genotypes included in this study varied considerably since the parents were purelines and their progenies were heterozygous in their third filial generation. In addition, the parents varied in species and maturity. Thus the materials showed a wide genetic base in phenological, physio-morphological characters, grain yield and its contributing characters. Variability in environments could be attributed to differences in terms of levels of organic matter, soil nitrogen and other soil nutrients, water regimes and management conditions among others.

The AMMI biplot classification of genotypes and environments revealed three mega environments; first, Matuga with a large positive IPCA1 scores; second, Msambweni drought with a large negative IPCA1 score and; third, Mtwapa and Msambweni no drought with small IPCA scores. Matuga and Msambweni drought had the highest discriminating power and were therefore good for selecting genotypes with specific adaptation while Mtwapa and Msambweni no drought were good for selecting genotypes that perform well across the test environment. The most high yielding and stable genotypes across the test environments were G41 followed by G1 and G34. The most unstable but high yielding genotypes demonstrating a strong GEI were G10 and G39. G10 was specifically suitable for Matuga while G39 was suitable for Msambweni drought condition.

7.4.2 The GGE biplot analysis

Although the environment main effect may contribute up to 80% or more of the total yield variation, it is usually the genotype main effect and the genotype x environment interaction (GEI) that are relevant to cultivar evaluation (Yan, 2002). The use of GGE biplots has been appreciated by many researchers in rice and other crops (Hagos and Abay, 2013; Kivuva *et al.*, 2014; Lakew *et al.*, 2014; Muthoni *et al.*, 2015) as it graphically displays general pattern of genotype responses across environments in multi-environmental trials data usually concealed in the general ANOVA. In this study, the GGE biplot results revealed that there was no correlation between drought and no drought test environments at Msambweni indicating that these two environments discriminated the genotypes differently. This was expected because although the two environments were established on the same location differences in water regimes and rainfall seasons contributed to lack of correlation. The drought environment was set up during the short rain season and drought developed from flowering to harvesting. In contrast, the no drought environment was set up during the long rain season and rainfall was adequate for growth and development of rainfed rice. This also implies that there is a need for separate breeding programmes for the short and long rain seasons. The distance between Mtwapa and Matuga from Msambweni drought environment was shorter than the distance between these two sites from Msambweni no drought environment. This indicated that Mtwapa and Matuga were more positively correlated to Msambweni drought environment than the no drought environment and therefore the three environments may have discriminated the genotypes similarly but different from Msambweni no drought condition. Mtwapa and Matuga environments were set up under upland aerobic conditions indicating that during growth and development the rice genotypes, under study, some level of stress similar to that observed at Msambweni drought condition may have developed.

Msambweni drought was close to the average environment and had the second longest vector after Msambweni no drought indicating that it discriminated among the genotypes and was representative of the whole target region. Based on the observation that Msambweni drought was positively correlated to Mtwapa and Matuga upland ecologies, this environment may be a good site for selecting genotypes with general adaptation for the upland ecology and drought tolerant genotypes for the lowland ecology. On the other hand Msambweni long rain season was discriminating and non-representative. This site is therefore good for selecting specifically adapted genotypes if the target environment can be divided into mega environments and/or for culling unstable genotypes if the target environment is a single mega environment.

The polygon view of GGE biplot is very useful for visualising the best genotypes in each environments and grouping environments for visualisation of possible crossover GEI and mega environments (Yan and Tinker, 2006). Different environments fall into different sectors, which imply that there are different high yielding cultivars for those sectors and it shows crossover GEI suggesting that the test environments could be divided into mega-environments (Yan *et al.*, 2007). In this study the environments fell into three sectors revealing the possibility of three mega environments and presence of crossover type of GEI. Msambweni drought and Mtwapa fell into one sector with G2 as the best performing genotype in this sector. Matuga fell into the second sector and the winning genotype was G37 while Msambweni no drought fell into the third sector with genotype G38 winning in this environment. Other researchers in sub-Saharan Africa have also appreciated the use of the polygon view of GGE biplot in identification of the best genotypes in different environments and revealing of possible mega environments among the test environments (Kivuva *et al.*, 2014; Lakew *et al.*, 2014; Muthoni *et al.*, 2015).

The biplot view of mean yield and stability revealed that the average grain yield of G37, G41, and G38 was higher than that of the average (ideal) genotype across the test environments. However, they had poor stability and were therefore good for specific adaptation. G37 was specifically adapted to Matuga while G38 and G41 were specifically adapted to Msambweni no drought condition. Advancing different F_3 populations for each mega environment would be more time and resource consuming than selection of the best one or a few populations for the whole target region. Genotype G39 followed by G40 combined high yield and stability across the test environments. These genotypes were therefore identified as candidates with general adaption for advancement to homozygozity simultaneously selecting within each population good performing pure lines for release in the region.

7.5 Conclusions

The AMMI and GGE biplot showed that the ranking of the genotypes changed across environments revealing a crossover type of genotype x environment interactions. Msambweni random drought and no drought environments were shown to be two independent environments suggesting the need for separate breeding programmes for the short and long rain seasons in the coastal lowlands of Kenya. Genotypes identified with wide and narrow adaptation differed between the AMMI and the GGE biplot graphical representations. The AMMI biplot showed that G10 was specifically adapted for Matuga, and G39 to Msambweni no drought environment while G41 followed by G1 and G34 were the most stable and high yielding genotypes across the test environments. In contrast, the GGE biplot showed that G37 was specifically adapted to Matuga, G38 to Msambweni no drought environment and G2 to Msambweni random drought environment and Mtwapa, while genotype G39 followed by G40 combined high yield and stability across the test environments. Since the results of this study are based on a single year data, and therefore may not be decisive, more temporal and spatial environments will be needed to give meaningful recommendations.

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General overview and conclusions of the thesis

8.1 Introduction

The overall objective of this study was to contribute to the expansion and intensification of rice production in Kenya through development of high yielding, widely accepted and adopted early maturing and drought tolerant cultivars. Pre-breeding experiments were set up to identify potential drought tolerant rice genotypes with farmers' preferred traits that could increase rice production in Kenya. Firstly, a survey was conducted in the rainfed lowland rice ecology in coast region of Kenya to identify farmers' desired traits and rice production constraints in Kenya. Secondly, popular landraces, local varieties, exotic interspecific and O*ryza sativa* L. rice lines were screened to identify drought tolerant genotypes. Thirdly, five interspecific and five O*ryza sativa* L. genotypes were selected as parents to determine gene action and inheritance of earliness, combining ability effects for phenological, grain yield and yield related traits and to assess the heritability, correlation and the direct and indirect effect of phenological, morphological and yield component characters on grain yield in rice. Finally, the magnitude of genotype x environment interaction (GEI) for grain yield in rice was estimated.

8.2 Research summary

8.2.1 Farmers' desired traits in rice cultivars and perceptions of production constraints to rice production in coastal region of Kenya

- Farmers desired high yielding, short duration and drought tolerant cultivars of medium height.

- Preference for short duration varieties means that farmers may plant two rice crops in the long rain season by, transplanting the second crop or possibly ratooning the first crop and one crop in the short rain season thus increasing rice production in the region.

- On grain quality traits, aroma and taste were the most preferred and desired phenotypic appearance of the grain was white, long and bold.

- Farmers also preferred rice cultivars with good baking qualities. Important traits for a variety with good baking qualities were; white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin while baking.

- Drought was ranked as the most important constraints and drought stress occurring at reproductive and grain filling stage was the most prevalent.

8.2.2 Genotypic variability of rice genotypes during reproductive stage under drought and no drought conditions

- Significant ($p<0.001$) differences among genotypes were observed for days to 50% flowering, spikelet fertility and grain yield per plant under drought and no drought conditions whereas significant ($p<0.001$) differences among genotypes were observed for relative leaf water content, canopy temperature, leaf rolling and leaf drying under drought conditions only.

- Among the medium to late maturing genotypes drought stress caused relative reduction in grain yield per plant of 57%, spikelet fertility (37%), relative leaf water content (34%) and relative increase in canopy temperature (19%).

- The mean leaf rolling and drying scores were 6 and 3 respectively while average delay in flowering was eight days.

- Two local cultivars, Shingo la Mjakazi and Kitumbo were moderately drought tolerant while genotypes NERICA-L-25, Tuliani and Kibawa Chekundu highly susceptible.

- The local cultivars Tuliani and Supaa were found to be potential donors for higher number of grains per panicle and heavy grains.

- Among the early maturing group, drought stress cause relative reduction in spikelet fertility of 34% with mean leaf rolling score of 4 and delay in flowering of five days.

- The genotype CT16323-CA-25-M was highly drought tolerant, NERICA 2 was moderately tolerant and CT16333(1)CA-22-M was drought susceptible.

- In both experiments, spikelet fertility was correlated with grain yield and the other physiological traits under stress and therefore identified as the most important trait to indirectly grain select for yield under drought conditions.

8.2.3 Inheritance of earliness in interspecific and *Oryza sativa* L. rice lines under drought and no drought conditions

- Significant variation ($p<0.001$) among genotypes was observed for days to heading, days to anthesis, days to maturity, number of productive tillers per plant and plant height

- Across environments, the earliest populations with 70 days to heading were CT16323-CA-25-M x Vandana and NERICA 1 x Vandana.

- The early class was dominated by crosses between E x E (8 populations) and E x EM (6 populations). The common parents were NERICA 2 appearing in 6 crosses and Vandana and CT16323-CA-25-M appearing in 5 crosses each.

- Fifty nine percent of the selected early maturing class were between interspecific and *Oryza sativa* lines.

- The F_3 populations, CT16323-CA-25-M x Vandana and Duorado x Vandana combined short duration with increased plant height and higher tiller number.

- There were significant GCA and SCA mean squares for all traits with an exception of non-significant SCA mean squares for number of productive tillers per plant under random drought conditions and plant height under no drought conditions.

- Under drought conditions, inheritance of earliness based on days to heading, was conditioned by non-additive gene action while under no drought conditions additive gene action prevailed. This was also observed for days to anthesis and plant height.

- For days to maturity and number of productive tillers per plant, additive gene action appeared to be more important under drought and no drought conditions.

- One interspecific line CT16323-CA-25-M and one *Oryza sativa* line, Vandana, consistently exhibited negative and significant GCA effects for shorter days to heading, days to anthesis and days to maturity under drought and no drought conditions, and across environments.

- Vandana combined earliness with good GCA for increased number of productive tillers per plant and plant height.

8.2.4 Combining ability for grain yield and yield components in interspecific and *Oryza sativa* L. rice pure lines under drought and no drought conditions

- Significant variation among genotypes was observed for a thousand grain weight, grains per panicle, panicle weight, weight of grains per panicle, grain phenotypic acceptability and grain yield

- The F_3 populations NERICA 1 x NERICA 2 and CT16323-CA-25-M x Vandana combined high yield potential (4 t ha^{-1}) with moderate drought tolerance index (1)

- Outstanding F_3 populations which combined higher yields with a higher a thousand grain weight, heavy panicle weight, heavy grains per panicle and a good grain phenotypic acceptability were NERICA 1 x NERICA 2, NERICA 1 x *Duorado* and NERICA 2 x *Duorado*.

- NERICA 1 x NERICA 2, yielded significantly higher than the parents at each environment and across environments and had a moderate relative drought index of 1.0.

- Among the selected high yielding F_3 populations 43% were crosses between interspecific x *Oryza sativa* lines and vice versa.

- The GCA mean squares for grain yield were significant under no drought conditions and non-significant under random drought stress conditions.

- There were significant GCA and SCA mean squares for the yield components under random drought and no drought conditions.

- The GCA/SCA predictability ratio (Baker, 1978) revealed that under stress and non-stress conditions non additive gene action was more important than additive gene action for grain yield, spikelet fertility, number and weight, of grains per panicle. In contrast, additive gene action was more important for a thousand grain weight.

- The line, Vandana, was found to be a good general combiner for grain yield contributing alleles for high grain yield to its progenies. The line *Duorado* precoce had the best GCA effect for a thousand grain weight. The interspecific line NERICA 2 was the best for number of grains per panicle while NERICA 1 had the best GCA effects for panicle weight, weight of grains per panicle and grain phenotypic acceptability.

- The mean performance of the parents did not necessarily correspond with their GCA effects for grain yield, spikelet fertility and grains per panicle and could not be used as an indicator of their combining ability.

8.2.5 Heritability, correlation and path coefficient analysis for grain yield and yield components in rice

- High levels of narrow sense heritability estimates were observed for days to heading (67%), days to anthesis (69%), days to maturity (90%) and for a thousand grain weight (82%).

- Narrow sense heritability estimates were low for grain yield (0.1%) and the other yield components; spikelet fertility (4%), number of grains per panicle (16%), panicle weight (0.7%) and weight of grains per panicle (0.5%)

- The traits, number of productive tillers per plant, panicle weight and spikelet fertility, were important direct contributors to yield improvement.

- A thousand grain weight had a high narrow sense heritability and exhibited a positive indirect effect on grain yield via panicle weight.

8.2.6 Genotype × environment interactions for grain yield in rice under no drought and drought conditions

- The study revealed a highly significant ($p<0.001$) genotype x environment interaction (GEI) effects for grain yield.

- The ranking of the genotypes changed across environments revealing a crossover type of GEI whereby the four environments fell into three mega environments

- The AMMI and GGE biplot analysis identified G37 (Luyin 46 x IR55423-01) as the highest yielding genotype across environments.

- Based on GGE biplot results, G39 and G40 combined high yield and stability across the test environments. Genotypes that showed specific adaptation were G37 for Matuga and, G38 and G41 for Msambweni no drought condition.

- Msambweni short rain season was positively correlated to Mtwapa and Matuga upland ecologies and was the most discriminating and representative of the test environments.

- Msambweni no drought condition was discriminating but non representative

8.3 Implications of the research findings

The results of this study revealed that farmers desired high yielding, early maturing and drought tolerant rice cultivars of medium height with white, long and bold grains. Unusual preferences were those of good baking qualities which included; white milled rice flour with low fat content, dough easy to work on, porous and does not stick on the baking tin while baking. On production constraints; drought, pests and diseases were ranked as the most important. Drought was common at reproductive and grain filling stages. These findings reveal that an opportunity exists in the coastal region to breed for high yielding, early maturing cultivars with drought tolerance at reproductive growth stage. However for faster adoption of the new rice cultivars incorporation of the desired grain quality traits is of paramount importance. Cultivars with good baking qualities were also on demand in the region which is another breeding opportunity.

There was considerable genetic variability for reproductive stage drought tolerance among the popular landraces, local cultivars, and exotic interspecific and *Oryza sativa* L. rice lines. Two local cultivars, Shingo la Mjakazi and Kitumbo which were moderately drought tolerant, the exotic genotype CT16323-CA-25-M which was highly drought tolerant and NERICA 2 which was moderately tolerant are potential donors for drought tolerance at reproductive stage. These genotypes are therefore recommended to be used in breeding programmes aimed at developing drought tolerant cultivars for the rainfed lowland and upland ecologies in sub-Saharan Africa.

Traits that were conditioned by additive gene action were days to anthesis, days to maturity a thousand grain weight and earliness based on days to heading, In addition, these traits had high narrow sense heritability estimates. Thus, they can quickly be improved under no drought conditions through recurrent selection procedures aimed at accumulating the desirable additive genes. On the other hand, the traits grain yield, spikelet fertility, grains per panicle and weight of grains per panicle were controlled by non-additive gene action and showed low narrow sense heritability estimates. Therefore, although selection based on these traits would not be effective in early generations but in the later generations, hybridization can be a choice for developing hybrids with high yield and desirable traits for the other yield components.

There was desirable combining ability for earliness, grain yield and yield contributing traits among interspecific and *Oryza sativa* L. rice lines. Generally the interspecific lines showed desirable GCA for earliness. Specifically, one interspecific line CT16323-CA-25-M and one *Oryza sativa* line, Vandana, consistently exhibited desirable GCA for earliness under drought and no drought conditions. In addition, Vandana, was found to be a good general combiner for grain yield, number of productive tillers per plant and plant height. Across environments, the line *Duorado* precoce had the best GCA effect for a thousand grain weight. The interspecific lines, NERICA 2 was the best for higher number of grains per panicle while NERICA 1 had the best GCA effects for heavy panicle weight and weight of grains per panicle, and excellent grain phenotypic acceptability. The specific crosses involving these parents may be subjected to early generation testing to identify plants with desirable characters that may be advanced to homozygozity followed by selection of best pure lines for release in the region.

Since the narrow sense heritability estimates for grain yield was low (0.1%) indirect selection for grain yield using other secondary traits would be the best option for its improvement. Although the traits, number of productive tillers per plant, panicle weight and spikelet fertility, showed a direct contribution to grain yield, the heritability estimates for number of productive tillers per plant (29%) was moderate, and low for panicle weight (0.7%) and spikelet fertility (4%) limiting their use in early generation selections. However, the study found that a thousand grain weight exhibited high narrow sense heritability (82%) and had indirect association with grain yield via panicle weight. It is recommended that within the outstanding crosses such as NERICA 1 x NERICA 2 , grain yield improvement begin in early generation by indirectly selecting for higher a thousand grain weight via heavy panicle weight. Moreover, a thousand grain weight had a positive and significant association with panicle weight though it showed a negative association with grain yield.

Even in the midst of large genotype x environment interactions, high yielding and stable genotypes do exist. Using the AMMI and GGE biplot models, high yielding and stable genotypes were identified. Across the test environments, the AMMI biplot showed that G41 (NERICA-L-25 x Vandana) followed by G1 (NERICA 1 x NERICA 2) and G34 (CT16323-CA-25-M x Vandana) as the most stable and high yielding genotypes. In contrast, the GGE biplot showed that G39 (Luyin 46 x IR74371-54-1-1) followed by G40 (NERICA-L-25 x IR55423-01) as the most stable and high yielding genotypes. However, since the results of this study were based on a single year data, and therefore may not be decisive, more temporal and spatial environments will be needed to give meaningful recommendations.

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