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Combining Ability for Drought Tolerance in Upland Rice Varieties at Reproductive Stage

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Abstract

Rice is an important food crop for human population ranking second among the mostly consumed cereal grains worldwide. Upland rice production is greatly constrained by drought stress resulting from rainfall variation patterns. Cultivation of drought tolerant varieties is considered the best option for drought management in rice production. The already released upland rice varieties are drought susceptible and have poor grain attributes hence, the aim of this study was to determine the combining ability for drought tolerance in upland rice. Four upland NERICA and two upland rice varieties were selected as parents for generating F_1s crosses following 6 × 6 complete diallel. The generated 30 F_1 crosses were advanced to F_2 population for field evaluation. The F_2 progenies together with six parents were planted in two sites; KALRO-Mwea Center Farm and Kirogo research Farm following a randomized complete block design in three replications. Drought stress was initiated 45 days after sowing after which data was collected on drought and agronomic parameters. The study revealed large genetic variations among the genotypes used. Both GCA and SCA were significant indicating the importance of both additive and non additive gene action in the expression of studied traits. In this study NERICA 2 and NERICA 15 were identified as good combiners for drought tolerance and grain yield under drought conditions. The single crosses namely; NERICA 15 × NERICA 2, NERICA 1 × NERICA 15, NERICA 11 × NERICA 15 and NERICA 2 × NERICA 15 were identified as superior for improving yield under drought conditions.

Keywords: combining ability, drought tolerance, rice (*Oryza sativa*)

1. Introduction

Rice is an important commodity and major food source for more than half of the world's population. With the ever increasing population, rice production must be increased by about 40% by 2025 to satisfy the growing demand without adversely affecting the resource base (Yogameenakshi et al., 2015). In Kenya, rice expansion and production in rainfed upland ecosystems is majorly constrained by abiotic and biotic stresses such as drought, low temperatures in highlands areas, low soil fertility, salinity and diseases such as rice blast (Menge et al., 2013). Following the recent climate variability and competing water for irrigation and other uses, rice production and expansion is likely to be more severely affected by drought. Rice succumbs to drought much faster than other cereals as it requires anaerobic conditions to complete its life cycle (Kumar et al., 2014). Thus, water shortage around flowering and grain filling stage reduces yield drastically as this affects various physiological mechanisms such as floral fertility in rice which is extremely sensitive to water stress (Boonjung & Fukai 2003; Kumar et al., 2014). Mitigation of drought by application of irrigation may be a more sustainable way for drought improvement though, this may not be effective since, rice irrigation is dependent on rainfall and in years of low rainfall, water supply is limited (Kimani, 2010). Consequently development of drought tolerant cultivars may effectively address the problem of frequent drought in rainfed upland ecosystem (Verulkar et al., 2010) because the crop provides huge opportunity to breed for drought tolerance due to its inherent capacity and wider adaptation in varied environments (Suresh et al., 2013).

Breeding for drought tolerance requires clear understanding of gene action and combining ability of the drought traits and yield components under water stress and non stress conditions. Given that, the success of any plant breeding programme fundamentally depends not only on selection of parents but also breeding methods (Can et al., 1997; Torres & Geraldi, 2007). Therefore, appropriate breeding methodology should be devised. The knowledge of combining ability is useful to assess nicking ability among genotypes and at the same time explicate the nature and magnitude of gene actions involved (Dar et al., 2014). Diallel (Griffing, 1956a, 1956b) and line × tester (Kempthorne, 1956) mating designs provide dependable information about the general and specific combining ability (GCA and SCA) of parents and their cross combinations and are helpful in estimating various types of gene actions (Verma, 2003).

Many previous studies showed that rice drought traits, rice yield related traits (tiller number, filled grains per panicle and grain weight) and agronomic characters (plant height and days to flowering) are inherited quantitatively and related genetically to one another and influenced by growing environments (Kobayashi et al., 2003). This necessitates the use of multi environmental trials for effective selection of promising lines. Therefore in the present study six parents with different tolerance to water stress were crossed in full diallel to assess the nature of gene action and combining ability for drought traits under drought conditions and non drought conditions and to identify the best combining parents as well as cross combinations for developing drought tolerant upland rice varieties in Kenya.

2. Materials and Methods

2.1 Germplasm

The germplasm consisted of four upland NERICA varieties and two upland rice varieties which were selected based on their drought tolerance, high yielding, disease tolerance (Rice blast) and good grain quality with aroma (Table 1).

Table 1. Rice genotypes used in the study

Variety	Source	Days to Maturity	GY (T/Ha)	Special Attributes
NERICA 1	KALRO* Mwea & Kibos	90-100	4.5	Aromatic, Blast tolerant, Long grains, Susceptible to drought
NERICA 2	KALRO Mwea	115	6.5	Non Aromatic and Drought tolerant
NERICA 11	KALRO Mwea & Kibos	90-105	7	Non Aromatic, Long grains, Tolerance to blast and susceptible to drought.
NERICA 15	KALRO Mwea	110	8	Drought tolerant and Non Aromatic,
SARO 5 (TXD 306)	KALRO Mwea	120	8.22	Aromatic, high yield ,Susceptible to drought
Komboka	KALRO Mwea	110	9.32	High yielding, mild aroma, tolerant to most diseases, Local adapted cultivar with good grain quality.

Note. KALRO: Kenya Agricultural Livestock and Research Organization.

Source: National crop variety list (KEPHIS, 2015).

2.2 Experimental Sites

Field experiments were conducted in Upland rainfed ecology during February to June 2016 at two different locations namely the KALRO Industrial Crop Research Center (ICRC) Farm Mwea and Kirogo Farm in Kirinyaga County, Mwea Sub-County, in Central Province (Table 2).

Table 2. Description of locations for experimental sites in KALRO Mwea and Kirogo Farm

Characteristics	Location	
	KALRO Center	Kirogo Farm
Latitude	00°32′ S	00°38′ S
Longitude	37°27′ E	37°22′ E
Elevation (Meters above sea level)	1159	1150
Annual rainfall(mm)	850	850
Annual maximum Temperature (°C)	28.6	28.6
Annual minimum Temperatures (°C)	15.6	15.6
Soil Type	Nitosol	Vertisols
Soil PH	5.65	5.07

Source: Soil analysis result by National Agriculture Research Laboratories (NARL).

2.3 Development of Crosses

In season 1 (January-December, 2015), six parents were grown in hybridization nursery at KALRO Mwea. The susceptible parents were crossed with the tolerant parents in a full diallel, thus producing 30 F_1 progenies and six selfed F_1 progenies. Emasculation of female parents was done using a vacuum emasculator machine that removes anthers from spikelets using suction pressure at 15 kPa. All the F_1 seeds generated from crosses were then planted in soil boxes at KALRO Center Hybridization Nursery. The panicles were covered with paper bags to prevent extraneous sources of pollen from getting to the pollinated plants. The mature seeds were harvested after attaining physiological maturity and dried up to 14% moisture content before planting in the field for drought evaluation.

2.3.1 Experimental Layout, Design and Crop Husbandry

During second season which was February 2016 to June 2016, the F_2 seeds and their six parents were planted in two sites in the field using randomized complete block design with three replications to screen them for tolerance to water stress and grain quality. Each genotype was grown in three row plots of 3 m length with inter row spacing of 20 cm and intra row spacing of 20 cm. The genotypes were grown in two sets of experiments namely; drought experiment and Non drought experiment (control). Diamonium phosphate (DAP) as a source of P was applied during planting at recommended rate of 60 kg P ha^{-1}. Thinning and gaping was carried out at 3-4 leaf stage to maintain single plant per hill at a spacing of 20 cm. The Calcium ammonium nitrate CAN as source of N 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 were effectively controlled using a synthetic pyrethroid. Three manual weeding were carried out at 20, 40, and 60 days after sowing. Harvesting was carried out manually.

2.3.2 Drought Experiment

Crops were watered twice a week and maintained at field capacity ranging between 0 kPa to -20 kPa until 45 Days after Sowing (DAS). At 45 DAS, stress was initiated by withholding irrigation and protecting the trial from rainfall by covering it with a rainout shelter. Plots were irrigated only when the soil water tension fell below -70 kPa at 30 cm soil depth. At this soil water potential, most lines wilted and exhibited leaf rolling and drying. This type of cyclic stress is considered to be efficient in screening for drought tolerance in populations consisting of genotypes with a broad range of growth duration and it ensures that, all lines receive adequate stress during reproductive development (Lafitte et al., 2004).

2.3.3 Non-Drought Experiment

From planting to physiological maturity, each plots received water twice per week. Thereafter, watering was done once per week to allow the plants to dry up for harvesting. Tensiometer was installed in all the three replications to monitor soil moisture that was maintained at field capacity ranging between 0 to -20 kPa throughout the growing period of the crop.

2.4 Data Collection

The standard Evaluation System (SES) for rice manual (IRRI, 2014) was used for all traits measured except where stated otherwise. Ten plants were randomly selected and tagged for data collection. One each plant, data were collected on:

➢ Days to 50% flowering (DTF) was recorded when 50% of the panicles of the plants of each plot had all anthers exerted.

➢ Chlorophyll content (Cc) was measured using SPAD meter at three different places in selected plants at 60, 75 and 90 days then averaged to express in lux units.

➢ Leaf rolling (LR) by measuring the drought response level on plant leaves which responded to -70 kPa water potential measured by a 30 cm underground installed tensiometers. When leaves completely curled in an O shapeleaf rolling was scored on a scale of 0 to 9: (IRRI, 2014) where; 0 - Leaves healthy; 1 - Leaves start to fold (shallow); 3 - Leaves folding (deep V-shaped); 5 - Leaves fully capped (U-shaped); 7 - Leaf margins touching (0-shape) and 9 - leaves tightly rolled.

➢ Leaf drying (LD) was scored at the end of the stress period in the morning. A scale of 0 to 9 was used based on a scale (IRRI, 2014). Where; 0 - No symptoms; 1 - Slightly tip drying; 3 - Tip drying extended up to ¼ length in most leaves; 5 - One forth to ½ of all leaves dried; 7 - More 2/3 of all leaves fully dried and 9 - All plants apparently dead.

- Spikelet fertility (SF) was determined as described by Lafitte et al. (2003). Seven panicles were randomly selected from each plot. The sample was dried and weighed using digital electronic balance, hand threshed and filled and unfilled spikelets were separated. Then filled grains and unfilled spikelets were counted.

The percentage fertile spikelet was calculated by the formula:

$$\text{Spikelet Fertility (\%)} = 100 \times \frac{\text{Number of filled grains in the sample}}{\text{Number of filled grains + Number of unfilled spikelets}} \quad (1)$$

- Days to maturity (DTM) were recorded as the number of days from planting to when 85% of the panicles in a plant were mature.
- Number of tillers per hill (NTL/H) was recorded by counting the number of productive tillers per hill.
- Panicle length (PL) was measured at maturity stage.
- Panicle Weight (PW) of the seven randomly harvested panicles at maturity stage was weighed by electronic weighing balance.
- Number of grains per panicle (NG/P) was obtained from the difference between the total number of spikelets and unfilled spikelets.
- Grain yield (kg ha^{-1}) Harvesting for GY was done at physiological maturity. Samples were harvested and dried in oven to 14% moisture before weighing, and weight converted to kg ha^{-1} then t ha^{-1}.
- Thousand grain weight (TGW) a thousand grains dried at 14% moisture content were weighed by electronic weighing balance.

2.5 Data Analysis

2.5.1 Analysis of Variance

The data was subjected to analysis of variance using Restricted Maximum Likelihood (REML) in GENSTAT 15th edition. Separation of genotype means was done by using the Fishers protected Least Significant Difference (LSD) at 5% level.

2.5.2 Combining Ability Estimates

The combining ability analysis was carried out as per Griffing's (1956a); Method 1, model I, in SAS Program 9.2 version. The replication and the blocks within replication were random while genotype was the fixed term. Means from REML analysis were used in a linear model regression to estimate GCA and SCA effects.The estimates of GCA and SCA of parents and progenies were calculated as:

$$\text{GCA effect } (g_i) = \frac{1}{n(n-2)} \; [nx_i - 2x \ldots] \quad (2)$$

$$\text{SCA effect } (S_i) = x_{ij} \; \frac{1}{n-2} (x_i + x_j) + \frac{2}{(n-1)(n-2)} x \quad (3)$$

Where, x_i, x_j = means of the i^{th} and j^{th} parents, respectively; $x..$ = grand mean; n = number of parent lines.

2.5.3 Combining Ability Estimates

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,

$$\frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA}} \quad (4)$$

Where, $2\sigma^2_{GCA}$ and σ^2_{SCA} are the variance components for GCA and SCA respectively estimated from Griffing's method 1 model I (fixed effects). Ratios close to one indicate additive effects and are important in the inheritance of the trait while ratios close to zero indicate dominance and epistasis effects which are important in the inheritance of the corresponding traits (Peyman et al., 2012).

3. Results

3.1 The Analysis of Variances under Drought Stress and Non-Drought Stress Conditions

Under drought environment, the mean squares showed that genotypes were highly significant at $P \leq 0.05$ for all characters. For environment × genotypes effects the mean square was also significant at $P \leq 0.05$ for all traits except Plant height, Number of tillers per hill and leaf drying (Table 3). Under non drought stress environment, the genotypes were highly significant at P ≤ 0.05 for all the traits. For environment × genotypes effects, the mean squares were significant at P ≤ 0.05 for only chlorophyll content and plant height (Table 4).

Table 3. Analysis of variance for various traits in Under Drought in KALRO Center and Kirogo farm

Source of Variation	df	Drought Parameters			Yield Traits		Other Agronomic Traits						
		LR (0-9)	LD (0-9)	SF (%)	TGW (g)	GY (T/Ha)	50% DTF	Cc (Lux)	PH (cm)	NTL/H	DTM (Days)	PW (g)	PL (cm)
Replication	4	1.7	0.4	209.7	23.03	2.33	23	26.3	120.8	20.46	201.44	18.9	3.7
Environment (E)	1	0.5	0.1	0.01	41.86**	41.86	234	0.31	0.01	0.01	31.89*	20.78	0.02
Genotype (G)	35	7.3***	0.39**	248.4***	100.56**	3.65***	396***	28.0**	656.1***	30.56***	143.47***	23.80***	9.5***
G*E	35	1.7***	0.29	161.8*	49.78***	2.33	61.9**	26.4***	0.01	15.2	190.68***	2.96***	8.0***

Note. * Significant at P ≤ 0.05, ** Significant at P ≤ 0.01 and *** Significant at P ≤ 0.001,LR - Leaf rolling, LD - Leaf drying, SF - Spikelet fertility, TGW - Thousand grain weight, GY- Grain yield, 50% DTF - 50% Days to 50% flowering, Cc - Chlorophyll content, PH - Plant height, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW- Panicle weight, PL - Plant length.

Table 4. Analysis of variance for various traits in Under Non Drought in KALRO Center and Kirogo farm

Source of Variation	df	Drought Parameter	Yield Traits		Other Agronomic Traits						
		SF (%)	TGW (g)	GY (T/Ha)	50% DTF	Cc (Lux)	PH (cm)	NTL/H	DTM	PW (g)	PL (cm)
Replication	4	341.9	37.3*	6.4	226.2	34.1	37.3	53.1	725.6	0.78	0.99
Environment (E)	1	0.21	0.13	1.4	416.7	186.4	0.16	0.41	0.11	0.21	0.17
Genotype (G)	35	60.30***	113.3***	3.70***	190.8***	20.1***	113**	11.80*	251.7***	8.4***	5.00**
G*E	35	83.4	0.1	2.8	182.0	21.5***	0.11	9.1	0.78	0.19	4.20*

Note. * Significant at P ≤ 0.05, ** Significant at P ≤ 0.01 and *** Significant at P ≤ 0.001,SF - Spikelet fertility, TGW - Thousand grain weight, GY - Grain yield, 50% DTF - 50% Days to flowering, Cc - Chlorophyll content, PH - Plant height, NTL/H - Number of tillers per Hill, DTM - Day to maturity, PW - Panicle weight, PL - Plant length.

3.2 Mean Performance for the Six Rice Parents under Non-Drought Conditions

Parent NERICA 2 (P_2) was the highest yielding with 5.2 t ha^{-1} followed by NERICA 1 (P_1) with 5.0 t ha^{-1} whereas Komboka (P_1) and Saro 5 (P_5) were the lowest grain yielders with 4.0 t ha^{-1} and 4.3 t ha^{-1} respectively. Parent P_2 had the highest spikelet fertility (85%) while; P_1 recorded the longest panicle length of 24.9 cm (Table 5).

Table 5. Mean performance for the parents under non drought in KALRO Center and Kirogo research farm

Parents	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
NERICA 1 (P_1)	84	1	1	29.5	5.0	80	47.0	24.9	14	109	5.0	128
NERICA 2 (P_2)	85	1	1	28.3	5.2	84	47.8	23.4	15	110	5.7	137
NERICA11 (P_3)	80	1	1	27.1	4.8	84	42.2	21.7	14	112	5.2	113
NERICA 15 (P_4)	83	1	1	29.7	4.8	83	46.5	24.2	15	113	5.6	140
SARO 5 (P_5)	78	1	1	19.6	4.3	80	42.5	23.2	17	128	4.5	86
Komboka (P_6)	79	1	1	20.7	4.0	72	44.7	23.3	16	134	2.7	105
Grand Means	81	1	1	26	4.6	90	45	23	15	118	5	118

Note. SF - Spikelet fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield; DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant height.

3.3 Mean Performance of the Generated Crosses under Non-Drought Conditions

The highest grain yielder crosses under non-drought condition were $P_2 \times P_4$, $P_1 \times P_2$ and $P_2 \times P_5$ with 5.6, 5.5 and 5.4 t ha^{-1} respectively. Moreover, these crosses had the highest number of reproductive tillers of 18, 16 and 17 tillers/hill respectively. The least in grain yield was $P_1 \times P_3$ and $P_2 \times P_6$ with 3.6 t ha^{-1} and 4.0 t ha^{-1}. Besides, low grain yield both crosses had the least spikelet fertility of 79% (Table 6).

Table 6. Mean performance for the generated crosses under non drought in KALRO Center and Kirogo research farm

Crosses	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
$P_1 \times P_2$	84	1	1	27.7	5.5	85	47.0	24.8	16	121	5.0	120
$P_1 \times P_3$	79	1	1	31.5	3.6	82	44.4	24.9	13	113	5.3	125
$P_1 \times P_4$	86	1	1	28.7	4.4	82	47.4	23.7	15	113	5.2	123
$P_1 \times P_5$	83	1	1	30.5	5.3	83	48.5	23.8	14	112	5.2	115
$P_1 \times P_6$	88	1	1	29.2	5.0	85	46.8	25.7	13	108	4.8	118
$P_2 \times P_3$	83	1	1	26.5	4.0	83	47.4	25.8	14	109	5.7	132
$P_2 \times P_4$	81	1	1	20.5	5.6	83	45.0	22.5	18	112	3.9	124
$P_2 \times P_5$	80	1	1	18.9	5.4	83	42.8	22.8	13	108	4.9	112
$P_2 \times P_6$	82	1	1	37.7	4.1	87	47.4	23.1	17	116	5.8	132
$P_3 \times P_4$	83	1	1	30.3	4.7	84	47.5	24.5	15	115	5.6	132
$P_3 \times P_6$	85	1	1	32.6	5.2	104	47.0	24.3	15	128	5.4	129
$P_3 \times P_6$	83	1	1	27.4	5.1	88	48.4	24.0	15	120	5.0	127
$P_4 \times P_5$	84	1	1	32.8	5.2	87	48.0	23.7	13	125	5.5	124
$P_5 \times P_6$	84	1	1	29.4	5.3	95	47.9	24.7	14	110	4.8	117
$P_4 \times P_6$	79	1	1	33.1	4.0	98	46.2	24.1	16	130	5.5	124
Grand Means	83	1	1	29	4.8	87	47	24	15	116	5.0	124
Overall Means	84	1	1	28	4.7	90	46	24	15	118	5.0	122
LSD (5%)	6.5	0	0	12.3	1.2	8.3	6.7	5.1	2.7	6.5	2.9	8.1
CV (%)	15.1	0	0	4.1	1.1	8.5	3.5	1.4	3.9	12.5	0.5	11.4

Note. P_1 - NERICA 1, P_2 - NERICA 2, P_3 - NERICA 11, P_4 - NERICA 15, P_5 - SARO5, P_6 - Komboka, SF - Spikelet fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield; DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle Length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant Height.

3.4 Mean Performance of the Six Rice Parents Crosses under Drought Conditions

Based on drought tolerance parameters, NERICA 15 (P_4) had high spikelet fertility with 81% followed by NERICA1 (P_1) with 75% and NERICA2 (P_2) with 74%. Parent NERICA 15 (P_4) and NERICA 2 (P_2) exhibited low scores of leaf drying and leaf rolling both with scores of 2. For grain yield parent NERICA 15 (P4) was the highest with 4.2 t ha^{-1} followed by NERICA 11 with 3.7 t ha^{-1}. On other hand SARO 5 (P_5) and Komboka (P_6) recorded low grain yield of 2.0 and 2.1 t ha^{-1}. Besides this low yield the two parents had lowest spikelet fertility and highest scores (5) of leaf rolling (Table 7).

Table 7. Mean performance for the parents under drought in KALRO Center and Kirogo research farm

Parents	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
NERICA 1 (P_1)	75	4	2	28.7	3.5	84	47.8	20.3	9	108	4.8	112
NERICA 2 (P_2)	74	2	2	24.6	3.7	85	46.7	24.8	9	113	4.6	105
NERICA11 (P_3)	73	4	2	24.0	3.4	86	45.5	21.8	8	111	4.6	99
NERICA 15 (P_4)	81	2	2	30.0	4.2	87	46.6	24.3	9	111	4.7	133
SARO 5 (P_5)	61	5	3	18.6	2.0	101	42.5	19.9	13	129	3.1	84
Komboka (P_6)	72	5	2	20.0	2.1	102	42.0	22.5	11	132	2.0	107
Grand Means	73	4	2	24	3.1	91	45	22	10	117	4	107

Note. SF - Spikelet fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield, DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant height.

3.5 Mean Performance for the Generated Crosses under Drought Conditions

Hybrid crosses of $P_3 \times P_4$, $P_2 \times P_4$ and $P_2 \times P_3$ exhibited high spikelet fertility and grain yield with 86, 83, 82% and 81% and a grain yield of 4.8, 5.2 and 4.6 t ha^{-1} respectively. Moreover, all these hybrids manifested low scores of leaf drying and rolling ranging between 2 and 3. The poor grain yielders were crosses such as $P_6 \times P_4$, $P_5 \times P_3$ and $P_5 \times P_1$ with 2.2, 2.0 and 3.0 t ha^{-1} respectively. The same crosses recorded low spikelet fertility of less than 70% and high morphological scores such as leaf rolling of 5 in all crosses (Table 8).

Table 8. Mean performance of the generated crosses under drought in KALRO Center and Kirogo research farm

Crosses	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
$P_1 \times P_2$	68	3	3	28.8	4.2	87	44.5	22.4	10	110	4.3	102
$P_1 \times P_3$	76	3	2	29.9	4.0	85	47.8	23.2	9	107	3.8	105
$P_1 \times P_4$	77	3	2	24.2	4.5	90	46.8	22.4	9	111	3.9	103
$P_1 \times P_5$	78	3	2	24.3	3.8	85	45.5	23.6	8	118	4.2	101
$P_1 \times P_6$	78	4	2	28.9	4.2	88	46.5	21.8	11	117	4.7	107
$P_2 \times P_3$	82	2	2	25.4	4.6	82	48.0	21.4	12	114	4.7	109
$P_2 \times P_4$	83	2	2	22.6	5.2	84	46.7	23.7	13	116	3.8	104
$P_2 \times P_5$	64	3	2	26.7	3.8	88	46.2	23.2	8	119	4.5	108
$P_2 \times P_6$	70	3	2	20.9	4.5	85	47.0	22.3	9	115	5.3	123
$P_3 \times P_4$	86	3	2	30.7	4.8	88	46.3	21.5	11	113	4.3	115
$P_3 \times P_5$	69	4	3	20.5	4.4	106	43.4	19.4	12	127	2.8	98
$P_3 \times P_6$	68	4	2	26.1	4.3	91	48.6	22.2	7	115	4.3	108
$P_4 \times P_5$	66	4	2	29.3	3.8	92	46.9	23.4	8	117	4.9	110
$P_5 \times P_6$	70	5	2	29.6	4.5	97	49.1	23.0	10	116	4.8	122
$P_4 \times P_6$	76	6	3	17.7	4.4	96	41.4	20.3	15	132	2.5	88
Grand Means	73	3	2	26	4.3	90	46	22	10	116	4	107
LSD (5%)	18	1.7	0.8	4.3	2.2	4.2	5.1	5.3	2.1	3.5	2.6	10
CV (%)	15	1	0.4	3.8	1.05	4.4	2.6	1.4	2.7	4.6	1.4	12

Note. P_1 - NERICA 1, P_2 - NERICA 2, P_3 -NERICA 11; P_4 - NERICA 15, P_5 - SARO5, P_6 - Komboka, SF - Spikelet Fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield; DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant height.

3.6 Analysis of Variance for Combining Abilities for Various Traits

3.6.1 Analysis of Variance for Combining Abilities for Various Traits under Drought Conditions

Analysis of variance of combining ability showed that the mean square of the GCA, SCA and RCA were significant at $P \leq 0.05$ for all drought tolerance traits, yield components and agronomic traits evaluated except days to maturity (Table 9). The variance for GCA includes the additive portion of the total whereas the variance for SCA comprises the non additive portion of the total variance as a result of dominance and epistasis. Non-additive gene action was predominant for spikelet fertility, leaf rolling, leaf drying, grain yield, thousand grain weights, chlorophyll content and number of tillers per hill. Additive gene action was predominant for days to 50% flowering, and panicle length. Plant height and days to maturity were governed by both additive and non additive gene actions (Table 9).

3.6.2 Analysis of Variance for Combining Abilities for Various Traits under Non-Drought Conditions

The mean squares of GCA, SCA and RCA were significant at $P \leq 0.05$ for all traits except spikelet fertility, chlorophyll content and days to maturity. Additive gene action was predominant for days to 50% flowering, panicle length and days to maturity while panicle weight and chlorophyll were governed by both additive and non additive gene actions (Table 10).

Table 9. Analysis of variance for combining abilities for various traits under drought in KALRO Center and Kirogo research farm

Source of Variation	df	Drought Parameters			Yield Traits		Other Agronomic Traits						
		SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (Days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
GCA	5	640.8**	18.9**	0.54**	98.8**	78.57**	1527**	32.4**	9.3**	40.8**	1956.5	98.8**	577.9*
SCA	15	229.5**	8.46**	0.32**	169.2**	113.3**	181**	37.8**	10.2**	25.3**	131.1	169.2**	1180*
RCA	15	139.6**	2.8**	0.40**	32.5**	69.5**	251**	16.8**	4.4**	13.8**	188.8	32.49**	158*
σ^2_A		3.9	0.01	0.003	0.25	0.1	0.68	0.5	0.26	0.17	3.01	0.01	0.001
σ^2_D		10.75	0.14	0.02	0.68	0.32	0.9	1.9	0.48	1.95	6.1	0.06	0.002
σ^2_A/σ^2_D		0.4	0.1	0.2	0.4	0.38	0.6	0.4	0.6	0.1	0.5	0.3	0.5

Note. * Significant at $P \leq 0.05$, ** Significant at $P \leq 0.01$ and *** Significant at $P \leq 0.001$, σ^2_A - Additive Variance, σ^2_D - Dominance variance, GCA - General combining ability, SCA - Specific combining ability, RCA - Reciprocal combining ability, SF - Spikelet fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY Grain yield, DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle Length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant height.

Table 10. Analysis of variance for combining abilities for various traits under non drought in KALRO Center and Kirogo research farm

Source of Variation	df	Drought Parameter	Yield Traits		Other Agronomic Traits						
		SF (%)	TGW (g)	GY (T/Ha)	50% DTF (Days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
GCA	5	20.2	89.1**	7.1**	412.6**	37.1	10.7**	15.2**	406.9	10.2**	89.1*
SCA	15	49.9	115.1**	1.5**	142.6**	17.5	4.6**	10.1**	350.3	10.7**	115.1*
RCA	15	96.2	119.6**	3.4**	92.8**	16.9	4.3**	6.25**	101.3	5.4**	119.6*
σ^2_A		0.54	0.24	0.02	6.7	0.5	0.07	0.08	3.01	0.02	0.46
σ^2_D		3.3	1.8	0.19	5.7	0.9	0.03	0.61	4.8	0.04	14.24
σ^2_A/σ^2_D		**0.2**	**0.2**	**0.2**	**0.7**	**0.5**	**0.8**	**0.2**	**0.6**	**0.5**	**0.1**

Note. * Significant at $P \leq 0.05$, ** Significant at $P \leq 0.01$ and *** Significant at $P \leq 0.001$, σ^2_A - Additive Variance, σ^2_D - Dominance variance, GCA - General combining ability, SCA - Specific combining ability, RCA - Reciprocal combining ability, SF - Spikelet fertility, TGW - Thousand grain weight, GY - Grain yield, DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle Length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant Height.

3.7 Combining Ability Estimates

3.7.1 General Combining Ability (GCA) Effects

The parent NERICA 2 (P_2), NERICA 1 (P_1) and NERICA 15 (P_5) had highest positive GCA effects for spikelet fertility of 3.41, 2.76 and 2.64 respectively (Table 11). Based on leaf rolling and leaf drying score NERICA 2 (P_2) and NERICA 15 (P_5) had the highest negative GCA effects of -0.78 and -0.07 for leaf rolling and -0.02 and -0.07 for leaf drying respectively. The highest grain yielder was NERICA 15 (P_4), NERICA 2 (P_2) and NERICA11 (P_3) with positive GCA effects of 0.8, 0.53 and 0.25 respectively. Besides, the two parents had minimum days to 50% flowering. In contrast, SARO 5 (P_5) and Komboka (P_6) had low GCA effect for spikelet fertility of 0.06 and -3.86 and positive GCA for leaf rolling and drying. Moreover, these two parents had negative GCA effects on grain yield in spite of showing positive GCA effect for number of tillers per hill of 1.18 and 1.14 respectively (Table 11).

Table 11. General combining ability (GCA) effects for observed traits under drought environment in KALRO Center and Kirogo research farm

Parents	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
NERICA 1 (P_1)	2.76***	-0.23	0.08	1.03***	0.04	-4.13***	0.74***	0.22	-0.93*	-4.28***	0.71***	-1.58
NERICA 2 (P_2)	3.41**	-0.78***	-0.02***	-0.1	0.53***	-4.13***	0.62***	0.49*	-0.57	-4.67***	0.45***	2.84**
NERICA 11 (P_3)	1.82***	0.3	-0.03	0.28	0.25	-5.54	0.12	-3.67	0.42	-2.67***	-0.03	0.04
NERICA 15 (P_4)	2.64***	-0.27***	-0.07***	1.32***	0.80***	-3.15***	2.09	0.18	-0.23	-4.7	0.52***	3.30***
SARO 5 (P_5)	0.06	0.56	0.15	-1.86***	-0.33***	7.14***	-0.97	-0.42	1.18***	7.2	0.24	-0.3
Komboka (P_6)	-3.86	0.41***	0.02	-0.66***	-0.18	4.06***	-0.59	-0.11	1.14***	5.86***	-0.17	-4.3

Note. * Significant at $P \leq 0.05$, ** Significant at $P \leq 0.01$ and *** Significant at $P \leq 0.001$, P_1 - NERICA 1, P_2 - NERICA 2, P_3 – NERICA 11; P_4 - NERICA 15, P_5 - SARO5, P_6 - Komboka, SF - Spikelet Fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield, DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle Length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant Height.

3.7.2 Specific Combining Ability (SCA) Effects

The specific combining ability was done for only crosses since, most of reciprocal crosses showed no significant effect for most of the traits evaluated. The hybrid $P_2 \times P_4$, $P_1 \times P_4$ and $P_2 \times P_3$ expressed high positive SCA effect for spikelet fertility of 5.37, 5.06 and 4.40 respectively. Moreover, $P_1 \times P_4$, $P_3 \times P_4$ and $P_1 \times P_3$ had low negative SCA effects for leaf rolling score. The best specific combiner for grain yield were $P_2 \times P_4$, $P_2 \times P_6$, $P_3 \times P_4$, with a positive SCA effects of 2.71, 1.27 and 1.19 respectively. Hybrid cross of $P_3 \times P_4$ had also good SCA effects for panicle weight while a cross of $P_2 \times P_4$, and $P_1 \times P_4$ exhibited good SCA for minimum days to 50% flowering (Table 12). $P_1 \times P_4$, $P_3 \times P_4$ and $P_2 \times P_4$ were overall best crosses for most traits evaluated. These crosses had positive value for leaf rolling in addition to thousand grain weight and 50% days to flowering (Table 12).

Table 12. Specific combining ability (SCA) effects for observed traits under drought environment in KALRO Center and Kirogo research farm

Crosses	Drought Parameters			Yield Traits		Other Agronomic Traits						
	SF (%)	LR (0-9)	LD (0-9)	TGW (g)	GY (T/Ha)	50% DTF (days)	Cc (Lux)	PL (cm)	NTL/H	DTM (Days)	PW (g)	PH (cm)
$P_1 \times P_2$	-3.04	0.38	-0.18***	-0.48	-0.49	-0.32	-1.69*	-0.02	1.18***	0.61	-0.53	-3.96
$P_1 \times P_3$	1.05	-0.37***	-0.26	2.09	0.69***	-3.32	1.02***	0.59	-0.56	-1.89	0.11	5.19*
$P_1 \times P_4$	5.06***	-0.47***	-0.05	-3.43***	-0.81	-1.04***	0.28	-0.64	0.43	-1.25	-0.39***	-6.36*
$P_1 \times P_5$	-0.18	0.6	0.19	-3.40***	0.04	2.80*	-0.76	-0.19	0.23	3.6	-0.35	-2.29
$P_1 \times P_6$	2.37**	0.96***	0.01	2.4	0.82***	3.4	-0.18	1.28	-1.78	3.5	0.24	-7.58
$P_2 \times P_3$	4.40***	-0.23	0.05	0.73	1.15	1.26	0.56	-0.68	0.58***	0.83	0.16	3.82
$P_2 \times P_4$	5.37***	0.67*	-0.01***	1.07***	2.71***	-1.29***	0.56	-0.61	0.15	-0.28	-0.3	-6.09*
$P_2 \times P_5$	-4.67	-0.51	-0.26*	2.23	0.43	-2.75***	-0.64	0.77	-1.97*	-3.19	0.03	1.87
$P_2 \times P_6$	-10.47	-0.35	0.2	-1.62	1.27***	-1.51	1.56***	-2.34	1.08***	-5.89	1.56***	20.86
$P_3 \times P_4$	0.76	-1.00*	-0.11	3.75***	1.19***	-2.21	0.69	-0.41	4.07***	-0.69	0.65***	4.80***
$P_3 \times P_5$	0.51	1.07***	-0.04	-4.38**	-0.95*	8.1***	-1.97*	0.09	2.2	5.14***	-1.14**	-5.44*
$P_3 \times P_6$	0.43	0.81	-0.01	1.44	-1.53	6.99	0.49	-0.64	4.07***	1.94	-0.83***	9.2
$P_4 \times P_5$	-0.47	-0.27	0.09	4.11	0.43**	-2.64***	1.63***	0.61	1.39***	-0.77**	1.03***	11.3
$P_5 \times P_6$	-4.8***	2.2***	-0.45	12.02***	-1.96***	10.91	5.54***	3.29	-3.62	-3.19**	1.69***	24.44
$P_4 \times P_6$	-7.91	2.42***	0.19	-8.7***	0.06	-2.63***	-4.69	-2.29	2.83***	11.97***	-1.6***	-41.41

Note. * Significant at $P \leq 0.05$, ** Significant at $P \leq 0.01$ and *** Significant at $P \leq 0.001$, P_1 - NERICA 1, P_2 - NERICA 2, P_3 - NERICA 11, P_4 - NERICA 15, P_5 - SARO5, P_6 - Komboka, SF - Spikelet fertility, LR - Leaf rolling, LD - Leaf drying, TGW - Thousand grain weight, GY - Grain yield; DTF - 50% Days to flowering, Cc - Chlorophyll content, PL - Panicle Length, NTL/H - Number of tillers per hill, DTM - Day to maturity, PW - Panicle weight, PH - Plant Height.

4. Discussion

The analysis for variance of various genotypes in different environments (drought and non drought) in both sites showed significant differences for all traits evaluated implying appreciable amount of genetic variability of the germplasm used in the study. Thus, the genotypes evaluated can be selected for genetic improvement for grain yield and other agronomic traits under drought conditions. Previous researchers have emphasized the importance of genetic variation in the breeding of new improved varieties (Ismaila et al., 2013; Falconer, 1981). Parents NERICA 2 yielded high in both conditions while NERICA 15 had high yield potential and drought tolerance traits only under drought conditions. This was further confirmed by the GCA estimates in which for both parents they were positive for spikelet fertility and grain yields and negative for leaf rolling and drying. Previous studies reported breeding potential for parents based on mean performance and GCA effects (Muthuram et al., 2012; Rad et al., 2012). In contrast, SARO 5 and Komboka had low mean performance for physiological mechanism of drought tolerance such as spikelet fertility percentages, leaf rolling and leaf drying as well as yield contributing components such as a thousand grain weight and panicle weight. This was an indication that, the two parents were drought susceptible and they were affected by low soil water moisture hence, grain yields were affected drastically (Lafitte et al., 2003).

The concept of combining ability as introduced by Sprague and Tatum (1942) is the capacity of a parent to transmit superior performance to its crosses. In this study, parents with high mean performance and positive GCA are preferred for positive traits of grain yields under drought condition. On the other hand, parents with low estimates and negative GCA are suitable for negative traits of grain yield such as plant height, leaf rolling, leaf drying and days to 50% flowering.

The combining ability analysis revealed significant GCA and SCA variance for most of the traits under drought and non drought conditions suggesting the importance of both additive and non additive gene actions in expression of these traits. Further analysis of GCA/SCA predictability ratio (Baker, 1978) revealed that drought tolerance traits such as spikelets fertility, leaf rolling, leaf drying and chlorophyll content in this study were governed by non additive genes in addition to other yield contributing traits such as grain yield, thousand grain weight and number of tillers per panicle. Similar results were reported in previous studies (Priya, 2003; Yogameenaki et al., 2015; Subramanian et al., 1998). Hybridization followed by selection in later generations may be recommended for improvement of traits controlled by non additive gene actions. The relatively higher magnitude of GCA variance (fixable genetic components) indicated the predominant role of additive gene action for traits like 50% days to flowering (0.6 and 0.7), panicle length (0.6 and 0.8) in drought and non drought conditions respectively. Previous research reported similar results (Kumar et al., 2007; Yogameenakshi et al., 2015). Simple selection procedure and pedigree breeding are sufficient to improve traits controlled by additive gene actions (Lavanya, 2000; Muthuram et al., 2012). In this study, NERICA 2 and NERICA 15 showed good general combiners ability for drought trait parameters, panicle length and grain yield. Similar findings were previous reported by Kumar et al. (2008) and Yogameenakshi et al. (2015).

Specific combining ability effects give the usefulness of a particular cross combination. To select high yielding variety under drought environment, crosses with few days to flower, high percentages of spikelet fertility, more tillers number per hill and low score for leaf rolling/drying can be selected. Crosses NERICA 15 × NERICA 2, NERICA 1 × NERICA 15, NERICA 11 × NERICA 15 and NERICA 2 × NERICA 15 were top ranked for one or more drought tolerant trait(s) and yield components. All these crosses had either or shared one of the good parent combiner with drought tolerance traits signifying that these crosses will eventually yield desirable transgressive segregants (Zhang et al., 1994; Li et al., 2002; Alam et al., 2004).

The present study showed that, none of the parents or the specific crosses were the best general combiners for all drought traits was good combiner for all the traits evaluated. This implies that the parents used in this study were genetically diverse and can be selected for different traits for further improvement. Previous research has reported similar findings (Singh et al., 2007; Panwar et al., 2005; Sharma & Mani, 2005).

Yield improvement in rice for drought prone environment is possible by selecting appropriate parents based on the mean performance and combining ability followed by suitable breeding programmes based on the nature of gene action involved (Muthuram et al., 2012; Yogameenakshi et al., 2015).

5. Conclusions and Recommendations

Drought tolerance traits namely the spikelets fertility, leaf rolling, leaf drying and chlorophyll content and the grain yield components like the grain yield, a thousand grain weight and number of tillers per panicle in this study were governed by non additive genes suggesting that hybridization followed by selection in later generations may be recommended for improvement of these traits. On the other hand, there was predominance of additive gene action effects among the traits such as plant height, panicle length and days to 50% flowering. In this study, two parents namely NERICA 2 and NERICA 15 were good combiners for drought traits, and grain yield components hence they could be utilized in hybridization program to introgress drought tolerance into elite lines. The crosses NERICA 15 × NERICA 2, NERICA 1 × NERICA 15, NERICA 11 × NERICA 15 and NERICA 2 × NERICA 15 also showed good SCA effects for one or more drought tolerant trait and yield components. Based on combining ability, none of the parents or specific crosses showed combination of all drought traits hence, to develop a drought tolerant genotype, a combination of desirable traits may be introgressed into adopted rice genotypes.

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