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Upland Rice Breeding in Uganda: Initiatives and Progress

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Additional information is available at the end of the chapter

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Abstract

Until recently, there was limited research on breeding upland rice varieties. Moreover, there is an increasing expansion of rice production from traditional irrigated production areas to rain-fed environments in the East African region, where drought problem is a serious challenge. To date, several initiatives aimed at increasing rice production have been made. Of the initiatives, promotion of upland rice production has been the most important in Uganda, but yield penalty due to drought continued to be a major drawback. This article traces progress in the upland rice breeding that started with improvement of late maturing varieties that had nonpreferred cooking qualities. Initially, introduced lines were evaluated and released. These varieties are the 'New Rice for Africa' (NERICA) that had been generated from interspecific crosses involving *Oryza glaberrima* and *Oryza sativa*. Several studies to understand the mode of gene action and modified pedigree breeding approaches for drought tolerance were conducted and used to develop new rice varieties. Up to 11 improved upland rice varieties were released and deployed in the country from 2002 to 2011 as a result of this initiative.

Keywords: drought tolerance, rice, gene action, NERICA, modified pedigree breeding

1. Introduction

Rice is an important food crop that is consumed mostly outside its major production areas in Uganda, with over 90% of production marketed to urban areas and major institutions within the country. This aspect makes rice to have a long value chain engaging several players. Rice is cultivated under rain-fed upland conditions, partly rain-fed lowland conditions and



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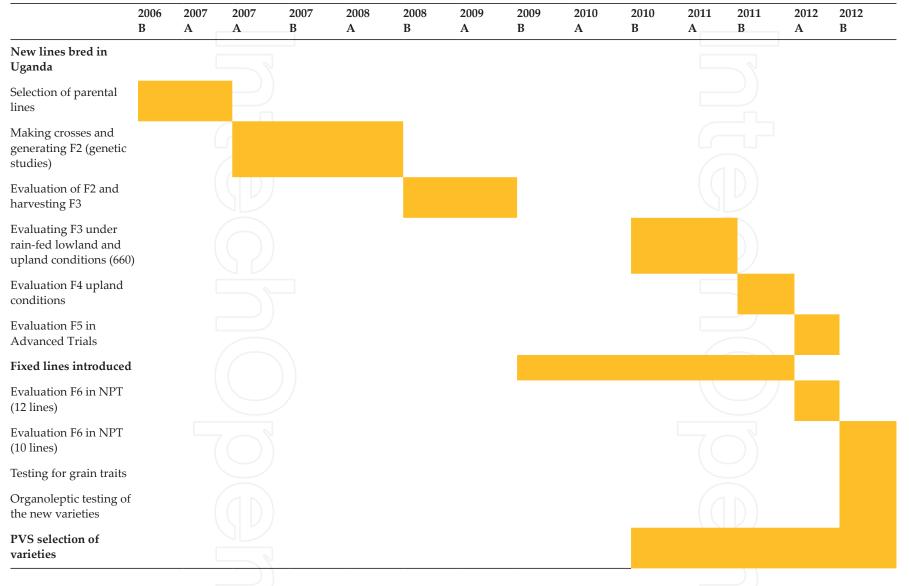


 Table 1. Timelines of [21]rice breeding activities 2006–2012.

irrigated conditions in Uganda, taking advantage of diverse ecosystems in Uganda [1]. Since the introduction of rice in 1904, Uganda had production under different agro-ecological conditions covering rain-fed upland conditions, partly rain-fed lowland conditions and irrigated conditions. Various production challenges are faced in these production areas.

New technologies are valuable for use in developing the new rice varieties globally including Africa. However, new tools can be most helpful if the existing varieties and candidate lines are properly characterized and documented. The purpose of this paper is to trace upland rice breeding efforts in Uganda and present for alignment, learning, and application in the new technology in their rice breeding programs with focus on breeding for drought tolerance and other stresses. This is critical considering that there is limited research on development of upland rice varieties suitable for production under mild drought conditions in the East African region and other similar Agro ecologies. There is also increasing expansion of rice production from traditional irrigated production areas to rain-fed environments, where drought problem is an inherent challenge. Indeed, drought emerged as a critical rice production constraint in East Africa [1, 2], particularly in Uganda [1], as promotion of upland rice was growing in the country.

Many upland rice varieties, earlier introduced in the country, were late maturing and did not have preferred cooking qualities. Later, more introduced lines were evaluated and released. These varieties had been generated through interspecific crossing involving Oryza glaberrima and Oryza sativa. These new genotypes were called the 'New Rice for Africa' (NERICA). They were resistant to major biological constraints but showed differential sensitivity to drought stress and new diseases, especially brown spot disease and narrow leaf spot disease. Besides, these varieties had nonaromatic characteristic which are the major concerns of the Uganda farmers. These factors made upland rice farmers to realize low yield mainly due to frequent drought stress. In addition, extensive use of irrigated rice come along with other limitations, namely need for environmental impact assessment and conflict on cultural values for use of the wetlands for farming. Subsequently, upland rice breeding involving adapted varieties led to new rice varieties with high resistance to biotic stresses and preferred agronomic traits [3]. However, abiotic stresses, especially drought stress remained a major constraint. Indeed, breeding for drought tolerance resistance in rice is challenging because the trait is quantitative and involves polygenes with low heritability. Modified pedigree breeding approaches were used in this breeding. In this paper, we review a trend of improvement of upland rice in Uganda covering three aspects: (1) screening of introductions for drought tolerance, (2) mode of gene action for drought tolerance, (3) evaluation of segregating lines, (4) Evaluation of promising lines, (5) variety release and status of deployment of the new generations of rice varieties in Uganda and within the African region. Detailed timelines of the activities are presented in Table 1.

2. Methodology

2.1. Screening of introductions for drought tolerance

A total of 191 rice introductions from major rice breeding centers were evaluated. Of the 191 materials, 77 were *O. sativa indica* comprising 45 from African Rice Centre (ARC), 15 lines

from International Rice Research Institute (IRRI), 13 from Mali, three from Uganda, and one from China. Among the introductions, there were three *O. glaberrima* accessions. The remaining 111 were interspecific lines developed from *O. sativa* × *O. glaberrima* crosses, comprising 18 from ARC and 93 the International Center for Tropical Agriculture (CIAT), Colombia coded as the CT series. However, among the interspecific samples, two genotypes namely WAB 880-1-27-9-2-P1-HB and WAB 450-24-2-3-P-38-1-HB were duplicates from different repeated introductions from IRRI and WARDA-Africa Rice Center. The 93 interspecific lines from CIAT were BC₄F₁s developed from crossing CAIAPO, a tropical *O. sativa* japonica from Colombia with RAM 24 (*O. glaberrima*).

This experiment was conducted at National Crop Resources Institute (NaCRRI), at Namulonge in central Uganda, at 00°32′ N latitude and 32°53′ E longitudes with altitude of 1150 m above sea level during dry season. The soils of the place are clay loam. The period December to March is characteristically the long dry season, but mean long term annual rainfall is 1270 mm.

In order to assess drought stress during reproductive growth stage, drought stress was imposed by terminating irrigation, when about 50% of the population had reached a point where interauricular distance between the flag leaf and penultimate leaf was zero [4]. It is the period when it is about 10 days before anthesis. It is the time when the penultimate leaves were fully expanded. Rainfall during the trial period was recorded. Irrigation was 14 days later, when 30% of the available water had been lost from the soil at 20-cm depth. The available soil moisture was taken using the ECHO soil moisture tester (Decagon Devices, Inc., Pullman, Washington, USA). All the grains from each panicle were hand threshed and dried. The filled and unfilled grains were then separated using floatation methods.

2.2. Mode of gene action for drought tolerance

This study investigated the nature of inheritance of drought tolerance in crosses between interspecific and intraspecific rice genotypes using secondary traits. Two separate experiments were conducted, using *O. sativa* and fixed interspecific lines derived from *O. glaberrima* and *O. sativa* crosses.

Experiment 1: Genetic studies on drought tolerance traits

The aim of the first experiment was to investigate the inheritance of drought tolerance at reproductive growth stage. Eighteen crosses were generated from two sets of 3×3 parents using the North Carolina mating design II (NCD II). All the 18 F2 and the 12 parents were evaluated in a 2×15 alpha lattice design with two replicates under a rain-out shelter and nonstress conditions in the field.

Thirty genotypes comprising 18 F2 progenies from sets, A and B, along with the 12 parents were used in this experiment (**Table 2**). The 30 entries were established in a rain-out shelter at National Crops Resources Research Institute (NaCRRI), Namulonge. The rain-out shelter was constructed using translucent sheets for the roof and wire mesh on the sides of the structure to prevent rain water and to allow free air circulation, respectively. In the rain-out shelter, standard troughs that are 1m wide, 8m long, and 1.5m deep were filled with soil for fallow field from Namulonge. Four troughs were made and filled with the soil, referred to as strips. The

Experiment	Crossing set	Genotype no	Breeding line	Туре	Parent type
1	SET A	18	CT 16334(2)-CA-2-M	Interspecific	Male
		105	WAB 365-B-1H1-HB	O. sativa	Male
		134	NERICA 9	Interspecific	Male
		138	NERICA 8	Interspecific	Female
		193	NERICA 13	Interspecific	Female
		196	IRAT 325	O. sativa	Female
	SET B	2	СТ 16346-СА-20-М	Interspecific	Male
		9	CT 16350- CA-5-M	Interspecific	Male
		12	СТ 16344-СА-9-М	Interspecific	Male
		96	Bonanca	O. sativa	Female
		121	WITA 2	O. sativa	Female
		129	CK 73	O. sativa	Female
2	SET C	18	CT 16334 (2)-CA-2-M	Interspecific	Female
		138	WAB 450-1-BL1-136-HB	Interspecific	Male

Table 2. Rice genotypes used for generating sets of F1 for drought tolerance.

seeds were planted in a 2 × 15 alpha lattice design. Two strips represented a replicate. The 12 parental genotypes were planted in three rows planted across the 1 m width strips, while the F2 populations were planted in six rows. The plant to plant spacing was 15 cm making plant population to be 36 for the parental lines and 72 for the F2 lines.

A second set of the 30 entries were planted in the field under optimal conditions. These conditions involved irrigating the field at 20 mm per week, during the period when there was no rain. In both trials, a 2 × 15 alpha lattice design planted in two replicates was used. Two seeds from each generation were drilled at a depth of 3 cm at spacing of 20 × 20 cm in each plot. In order to reduce border effects, 20 cm was left between plots. The 12 parental genotypes were planted in 5-row and 3-column plots, while the F2 populations were planted in 5-row and 6-column plots. Overall, there were 15 plants per replicate of the parents and 30 plants per replicate of each F2 genotype, thus the total number of plants were 30 and 60 for the parents and F2, respectively. The plants were thinned to one plant per hill. Standard cultural practices including hand planting and hand weeding were followed. The crops were fertilized with 25 kg N ha⁻¹ at 20–25 days after transplanting (DAT) and the same rate at 40–45 DAT to enhance plant vigor.

Drought stress was imposed by terminating irrigation, when about 50% of the populations had attained an interauricular distance between the flag leaf and penultimate leaf of zero, that is the period about 10 days before anthesis [4, 5]. This method of identifying the stage of imposing drought was applied both in the field and in the rain-out shelter. In general, this is the time when the penultimate leaves were fully expanded. Rainfall during the trial period was recorded.

In the field experiment, irrigation was applied using sprinkler irrigation. The field was irrigated, every three days before imposing drought stress. On the day the irrigation was terminated, the field was irrigated to field capacity in the evening between 5:00 and 6:00 pm, which was resumed 14 days after its termination using sprinkler irrigation. The duration of drought stress was determined by testing the level of soil moisture daily, using the ECHO soil moisture tester (Decagon Devices, Inc Pullman, Washington USA). On the day, when 30% of the available water had been lost from the soil at 20-cm depth, irrigation was resumed. In the rain-out shelter, water was applied using hand irrigation cans but water was calculated for each strip at 140 L per week, which is equivalent to 20 mm per week.

The number of filled grains was counted per panicle at grain maturity period. Two panicles from each plant were randomly collected and record of number of filled grains was determined using floatation method described by these authors [6].

Experiment 2: Generation means analysis (GMA) for filled grains in rice

In the second experiment, the magnitude and direction of gene action for drought tolerances at reproductive stage was determined in five populations P1, P2, F1, F2, and F3 generated from a drought tolerant × susceptible cross using generation mean analysis (GMA). They are in set C (**Table 2**). The materials were planted in the dry season and drought was imposed by terminating at the stage of panicle initiation.

In this experiment, all the five populations generated from crossing; parents P1 and P2, their F1, F2 and F3 genotypes were planted following a randomized complete block design (RCBD) with two replicates. Two seeds from each generation were drilled at a depth of 3 cm at spacing of 20 × 20 cm in each experimental unit (plot) in the field at NaCRRI. The generations P1, P2, and F1 were planted in 5-row and 3-column plots, while F2 and F3 were planted in 5-row and 6-column plots. Overall, there were 15 plants per replicate of the parents, 30 plants per replicate of each F2 genotype, thus the total numbers of plants were 30 and 60 for the parents, F2, respectively. The cultural practice in experiment 1 was followed, and drought stress was imposed following procedures in experiment 1.

2.2.1. Data analysis

Data was analyzed in three parts, namely analyses of variance, residual maximum likelihood (REML), regression, and generation means. The analysis of variance was performed for different traits associated with drought tolerance in the two sets of populations, A and B, pooling for both stress and nonstress environments. Using REML, the separate sets were analyzed for each trait. The analyses of the variance components of genotypes were further partitioned into variations, due to parents and crosses.

General analyses of variance were performed for filled grains, grains per panicle, leaf area, plant height, tiller number, and panicle number of all hybrids including checks. Genetic analyses for the six parameters of experimental hybrids were then performed in GenStat [7] as a fixed effects model across two locations [8] as follows:

Generation mean analysis of the genotypes CT 16334 (2)-CA-2-M crossed with WAB 450-1-BL1-136-HB was used to determine additive, dominant, and epistatic effects following the

model [9]. The various generations did not have equal variances; therefore, weighted inverse of the variances was used in subsequent analysis according to these authors in Ref. [10]. Regression analysis procedures were used to find the best fit model. It is a graphical method used to compare the additive model with additive-dominance models. Any effect that was not significant at 5% level was excluded from the model. The parameters were fitted using weighted mean squares as described by Ref. [11].

A scaling test was conducted using linear combinations of various means according to Refs. [9–12] to detect the presence of nonallelic interactions that are known to bias estimates of additive and dominance components in the populations when present. However, in this case, where F3 populations are used instead of backcross populations, the additive effects estimate is for both additive effects and additive × additive interaction effects. Similarly, the dominance effect combined both dominance effects and dominance × dominance interaction effects as a single estimate [12]. This is not a major drawback considering that most breeding work exploits additive effects and dominance effects. Standard errors of generation means were computed by performing nested analysis of variance following methods used in Ref. [13].

In order to verify the number of genes involved in the transmission of traits associated with drought tolerance, Castle-Wrights formulae described in Ref. [14] was used.

2.3. Evaluation of segregating lines

2.3.1. Preliminary evaluation 1

Preliminary yield trials were conducted on station with objective of varietal screening, evaluation, and seed increase. These were F3 selections from the previous experiment. Overall 660 genotypes were selected from the F3 generation based on field performance. All the seed from each of the 660 hills of F3 genotypes were divided into three sets. One set was remnant; a second set was planted in the rain-fed low-land environment, while the third set was planted under rain-fed upland conditions, all on station within Namulonge. The planting was in November, 2010. All the seed from each hill was planted to 5-m long rows and evaluated.

The second set was planted under rain-fed low-land with ample moisture throughout the growth period of the lines. The evaluation focused on maturity period, tillering capacity, presence of foliar diseases, and physical grain characteristics. Lines that had longer maturity period than the variety NERICA-4, number of reproductive tillers less than 5 per hill, presence of foliar diseases, and grain discoloration were eliminated. Besides, infection by common pathogen namely rice blast, bacterial leaf blight, grain discoloration, and sheath rot were used to eliminate lines. The team that evaluated the materials comprised of scientists, farmers, and rice field workers.

The third set comprising all the 660 lines was planted under rain-fed upland conditions. Selection was made as previously stated for rain-fed low-land conditions. Unlike selection under rain-fed lowland conditions where a minimum of seven productive tillers was considered acceptable, in this production environment, five productive tillers was considered the minimum.

2.3.2. Preliminary evaluation 2

Set 1: Evaluation of 84 rain-fed lowland rice lines: a total 84 lines of F4 segregating populations were selected from the 660 F3 lines genotypes and planted in five sites namely Namulonge, Kigumba, Kibaale, Lira, and Doho. Each entry was planted in a 3 × 18 alpha lattice design at spacing of 20 × 20 cm planted in rows five plots each 5-m long. The evaluation had three main objectives. The first objective was to test the new genotypes under varying stress conditions. The major biotic and abiotic stresses targeted were drought stress, rice blast, RYMV, BLB and Leaf Streak, narrow leaf spot and brown leaf spot. The locations selected were major rice growing areas that had had the production constraints. The second objective was to assess yield of the whole set at Namulonge site. The third objective was to identify farmer preferred varieties using participatory variety selection method.

2.4. Evaluation of promising lines

2.4.1. On-farm evaluation

On-farm trials were conducted through participatory and multilocational testing of selected upland varieties. Selection of sites for participatory and multilocational testing considered the following: (i) key representative ecological zones, (ii) participation of stakeholders, and (iii) availability of resources to effectively conduct the exercise. Seed companies were invited and a proposed method of allowing most seed stakeholders to participate in variety evaluation was adhered to. Twenty lines that were tested in 2011B in two locations namely Namulonge and Kibaale. Subsequently, 12 lines were tested in 2012A and finally 8–10 in 2012 B.

In order to identify suitable upland rice varieties, the best rice lines from preliminary trials were submitted to advanced yield trial (AYT). These genotypes were WAB 95 B-B-40-HB (the best performing line among lines received through STRASA and two best lines selected from Upland Regional performance trial (ART3-11L1P1-B-B-2 and ART8-L15P14-1-2-1) as well as three genotypes that performed well among 600 new lines developed at Namulonge. The 2011 season II was suitable for selecting high yielding diseases resistant. For instance, WAB95-B-B-40-HB and WAB788-16-3-2-1-HB earlier selected had considerable symptoms of BLS and narrow leaf spot.

2.5. Variety release and status

In the year 2013, six best performing rice varieties were presented for release to the Variety Release Committee in Uganda. Among the traits and Characteristics that was provided as evidence of superiority to the existing rice varieties were, higher yield, preferred grain and cooking qualities, maturity, tolerance to stresses especially drought.

3. Results

3.1. Screening introductions for drought tolerance

A list of only 30 genotypes, including top 20 and bottom 10 least performing genotypes, in terms of filled grains are presented in **Table 3**. Among the top 20 genotypes, three namely

No.	Genotypes	Filled grains (%)
Гор 20 genotypes		
112	WAB 56-50	96.3
53	CT 16333(1)-CA-18-M	91.1
4	CT 16326-CA-3-M	89.1
01	NERICA 14	88.7
08	WAB 56-39	88.6
37	NERICA 7	88.1
32	CO 39	87.8
42	VANDANA	87.6
24	NERICA 6	87.4
3	CT 16340-CA-9-M	86.7
90	NERICA 17	86.6
5	CT 16329-CA-10-M	85.5
77	WBK 35 (F3)	84.9
2	CT 16315(1)-CA-1-M	84.7
	CT 16330(1)-CA-2-M	84.1
65	IR 64	83.8
88	NERICA 15	83.5
)	CT 16307-CA-5-M	83.5
0	CT 16353-CA-17-M	83.4
0	CT 16324-CA-10-M	83.1
ottom 10 genotypes		
69	IR 57514-PMI 5-B-1-2	49.4
0	CT 16316-CA-2-M	49.4
06	IDSA 6	49.1
04	ITA 123 (FKR 28)	47.9
75	RAM 118	47.8
9	CT 16346-CA-11-M	47.8
2	CT 16312(1)-CA-1-M	47.3
66	IR 77298-14-1-2	45.7
55	LAC 23	43.8
5	CT 16307(1)-CA-2-M	27.9

No.	Genotypes	Filled grains (%)
Overall	Mean	67
	LSD _{0.05}	1.88
	CV%	13.2
	Range/LSD	17.6
	Variance	18.6
Table 3. The top 20 and bottom 1	0 genotypes in terms of percent filled gra	iins.

NERICA 7, CO 39, and VANDANA were reference materials for high drought tolerance at reproductive growth stage. There were nine out of the 20 lines from the CT breeding lines and five from the NERICA generations.

3.2. The mode of gene action for drought tolerance

3.2.1. Gene action

Generalized linear analysis for different traits pooled across sets and sites are presented in **Table 4**. Results showed that both GCA and SCA effects within sets for filled grains, grains per panicle, leaf area tiller number, and number of panicles per plant were significant (P = 0.001), while only the GCA effects within sets for tiller number were significant (P = 0.001) but not the SCA effects.

The male and female mean squares were all significant (P = 0.05) for the filled grains under drought stress (DS) and nondrought stress (NDS) conditions for the A set population (**Table 5**).

Source of	Mean square value									
variation	d.f	Spikelet fertility	Grains per panicle	Leaf area	Plant height	Tiller number	Panicle number			
Env ¹	1	146.5***	1441.2***	1335.9***	109.3***	1534.8***	1708.8***			
Set	1	41.5***	13.6***	35.0***	10.1***	0.7	14.1***			
Set/GCA _f	4	10.1***	10.5***	17.3***	7.3***	3.2**	5.1***			
Set/GCA _m	4	5.8***	11.4***	12.8***	26.5***	8.3***	3.8**			
Set/SCA	8	3.6***	8.5***	8.3***	26.5***	1.2	14.6***			
Env × Set	1	14.9***	15.4***	35.4***	1.9	6.3**	13.2***			
Env × Set/GCA _f	4	14.8***	8.4***	14.7***	1.4	4.5***	0.3			
$Env \times Set/GCA_m$	4	5.6***	7.9***	11.9***	3.7**	2.5**	0.1			
Env × Set/SCA	8	2.8**	7.2***	8.3***	1.8	1.6	0.5			

^{**} P < 0.01.

*** P < 0.0010.

Table 4. Pooled mean square for filled grains and other secondary traits under drought stress and nondrought stress environments.

¹ Environment.

		Mean square values for sets A and B						
		Set A		Set B				
Source	d.f	Drought stress	Nondrought stress	Drought stress	Nondrought stress			
Fertility ¹								
Male	2	3.21*	12.90*	0.51*	1.86			
Female	2	4.07^{*}	9.01*	2.58*	5.40			
Male × female	4	1.56	6.84*	3.29*	0.80**			
Total grains per panicle								
Male	2	4.58^{*}	8.60***	2.39	12.28***			
Female	2	4.14^{*}	9.86***	1.38	9.51***			
Male × female	4	2.64*	9.40***	0.62	5.83***			
Leaf area								
Male	2	3.09*	11.00***	6.96***	15.51***			
Female	2	1.40	16.21***	10.01***	16.01***			
Male × female	4	4.76***	9.74**	17.74***	5.34***			
Plant height								
Male	2	4.46^{*}	4.45	26.70***	26.44***			
Female	2	1.26	1.20**	7.66***	7.27***			
Male × female	4	8.14***	8.14***	15.70***	14.70***			
Tiller no								
Male	2	23.13*	42.99	26.70***	4.61**			
Female	2	3.36	49.08	7.66***	0.75			
Male × female	4	2.17***[23]	13.97	15.70***	1.67			

¹ Filled grains in percentage.

Table 5. Mean squares for filled grains, total grains per panicle, leaf area, plant height, and tiller number under drought and nondrought stress.

There was significant (P < 0.05) mean square for male × female interaction for the filled grains under NDS for set A. In the case of the B crossing set, the male × female interaction mean squares were significant under DS and NDS conditions. In addition, the mean square of male and female were significant under DS but not under NDS. The male, female, and male × female interaction mean squares were all highly significant (P = 0.001) for the total number of grains per panicle under NDS conditions for the A set and significant (P = 0.05) under DS conditions. In the case of B crossing set, male, female, and the male × female interaction, mean squares were significant under NDS conditions, but not the case under DS conditions. The set A had highly significant (P < 0.001) male, female, and male × female mean squares for leaf area under NDS conditions. Mean squares for male and male × female interactions were significant for leaf area under DS conditions, but not the case of female mean square. The results of the B crossing set revealed that male, female, and the male × female interaction mean squares were all highly significant (P < 0.001) under the NDS and DS conditions.

The male × female interaction mean squares were all highly significant (P = 0.001) for the plant height under DS, and NDS conditions for the A and B populations. There was significant mean square for female effects under NDS, but not under DS conditions for the A and B populations. In the case of B crossing set, male, female, and the male × female interaction mean squares were all highly significant under both NDS and DS conditions. Mean squares for male, female, and male × female interaction mean squares were not significant for the tiller number under NDS conditions for the A populations. There was, however, significant mean square for male and the male × female interactions but not female mean squares under DS conditions. On the other hand, the B crossing set had male, female, and the male × female interaction mean squares, all highly significant, under both DS and only the male under NDS conditions.

3.2.2. Relative contribution of GCA and SCA

General combining ability (GCA) for female and male (GCA_f and GCA_m) in A populations under DS and NDS conditions are presented in **Figure 1**. The total GCA for both male and female parents (GCA_t) under DS were more than 55% for all five traits except leaf area that had 42%. All the SCA values were less than 50%. The SCA effects of tiller number, under DS, was 14% and the male × female interaction was not significant (**Table 5**). Similarly, the SCA effects for filled grains were not important under DS conditions because there were lack of significance (**Table 5**). This finding, therefore implies that the additive effects was more important than nonadditive effects for filled grains, total number of grains per panicle, plant height, and tiller number.

Under NDS, however, filled grains, leaf area, and tiller number had GCA_t more than 55%. The total number of grains per panicle and the plant height had nearly equal GCA_t, when compared with SCA. This finding implies that the additive effects are more important than nonadditive effects for filled grains, leaf area, and tiller number, while additive and nonadditive effects had nearly equal effects for total number of grains per panicle. However, the lack of significance in the male × female interactions for tiller numbers (**Table 5**) makes the importance of SCA not valid.

Results of the GCA effects for female and male (GCA_t and GCA_m) for B populations, under DS and NDS conditions, are shown in **Figure 2**. The GCA total (GCA_t) under drought was more than 55% for filled grains, total number of grains per panicle, and tiller number under DS. The GCA_t and SCA for plant height were nearly equal, while a very high SCA value of 68% was found for leaf area. All the SCA values were less than 50%; moreover, the SCA effects for tiller number were not significant (**Table 5**) and that of total number of grains per panicle were also not significant (**Table 5**). This finding implies that the additive effects were more important than nonadditive effects for filled grains, total number of grains per panicle, and tiller number, while additive and nonadditive effects had nearly equal effects for plant

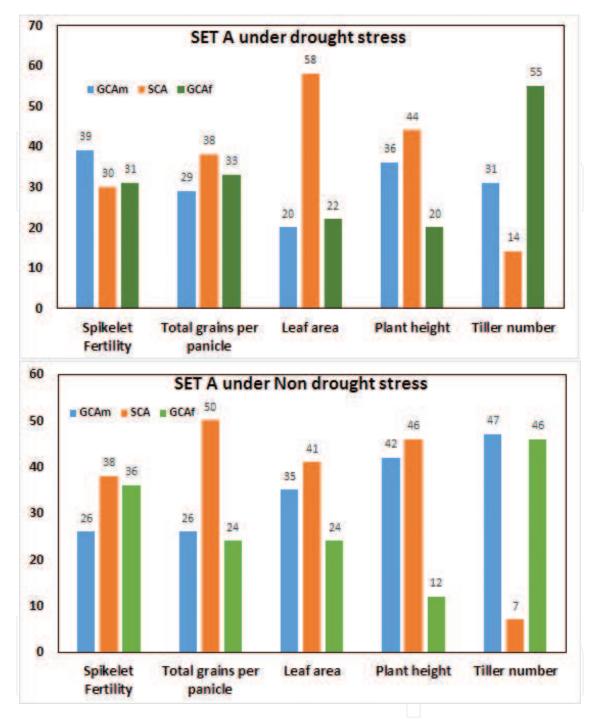


Figure 1. Relative (%) contribution of GCA and SCA effects to the cross sum of squares in set A under drought stress and nondrought stress.

height. Under NDS conditions, however, filled grains, total number of grains per panicle, leaf area, and tiller number had GCA_t more than 55%. The plant height had nearly equal GCA_t when compared with the SCA. This finding implies that the additive effects were more important than nonadditive effects for filled grains, total number of grains per panicle, leaf area and tiller number, while additive and nonadditive effects had nearly equal effects for plant height.

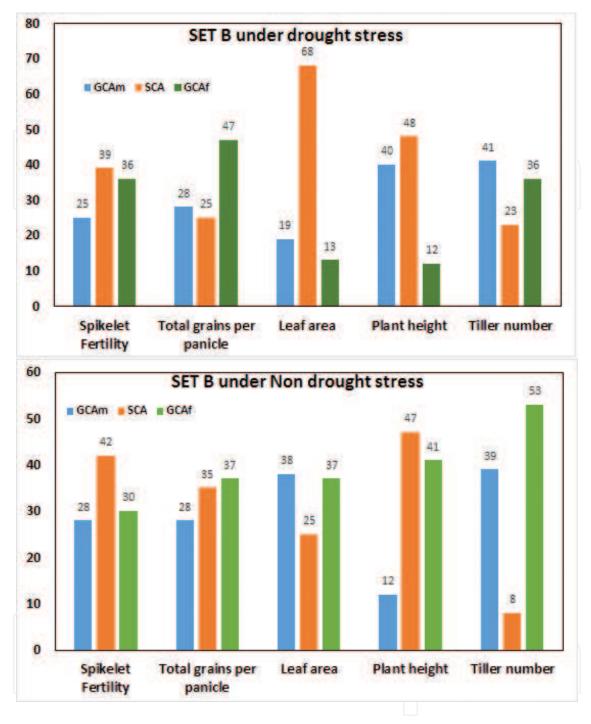


Figure 2. Relative (%) contribution of GCA and SCA effects to the cross sum of squares in set B under drought stress and nondrought stress.

3.2.3. General combining ability effects

Table 6 showed the GCA effects for filled grains for interspecific and intraspecific rice. The GCA values for filled grains were the only one presented, because other secondary traits had weak correlation with the filled grains, which is a trait associated with drought tolerance. Positive GCA effect is desirable in breeding for improved drought tolerance. Strong negative

	Filled grains				
	Nondrought stress	Drought stress			
Female					
NERICA 8	-0.46	-3.42**			
NERICA 13	-1.69	3.45**			
IRAT 325	2.15*	-0.03			
Bonanca	-2.80**	1.04			
WITA 1	-4.98***	-6.23***			
CK 73	-2.18*	5.19***			
Male					
CT 16334(2)-CA-2-M	-1.29	-1.18			
WAB 365-B-1H1-HB	-0.71	-2.12*			
NERICA 9	2.00^{*}	3.30**			
СТ 16346-СА-20-М	-2.54**	-2.26*			
CT 16350- CA-5-M	5.26***	-1.16			
CT 16344-CA-9-M	-2.72**	3.42**			
	±0.83	±0.97			

Table 6. Estimates of general combining ability (GCA) effects for filled grains under drought and nondrought stress conditions.

values of GCA effects of parents show contribution of GCA towards low filled grains, while high positive values show high filled grains. Since both GCA effects and SCA effects were significant for filled grains, the individual values for both GCA and SCA effects are presented (**Tables 6** and 7). Parents CT 16350- CA-5-M, IRAT 325, and NERICA 9 had positive and significant scores of filled grains under NDS conditions. In the DS environment, CK 73 was highly positive and significant at P = 0.001, while CT 16344-CA-9-M, NERICA 9, and CT 16346-CA-20-M had positive and significant filled grain scores at P = 0.01.

3.2.4. Specific combining ability effects

Superior crosses were observed, with positive SCA effects (**Table 7**). Under nondrought stress conditions, crosses WITA 1 × CT 16350- CA-5-M, Bonanca × CT 16346-CA-20-M, and CK 73 × CT 16344-CA-9-M had significant filled grain score of 0.01%, 0.01%, and 0.001%, respectively. The cross WITA 1 × CT 16344-CA-9-M had significant filled grain score at 0.05 level of significance. In the drought stress conditions, the cross NERICA 8 × WAB 365-B-1H1-HB were highly significant at P = 0.001, and Bonanca × CT 16344-CA-9-M and IRAT 325 × CT 16334(2)-CA-2-M were positive and significant at 0.01.

	Filled grains	
	Nondrought stress	Drought stress
NERICA 8 × CT 16334(2)-CA-2-M	-3.46	-12.86***
NERICA 13 × CT 16334(2)-CA-2-M	1.47	4.48^{*}
IRAT 325 × CT 16334(2)-CA-2-M	0.73	7.21**
NERICA 8 × WAB 365-B-1H1-HB	-0.59	8.53***
NERICA 13 × WAB 365-B-1H1-HB	-2.01	-4.93*
IRAT 325 × WAB 365-B-1H1-HB	1.90	-5.71*
NERICA 8 × NERICA 9	3.60	0.92
NERICA 13 × NERICA 9	-1.12	3.91
IRAT 325 × NERICA 9	-0.46	-1.52
Bonanca × CT 16346-CA-20-M	6.15**	-3.19
WITA 1 × CT 16346-CA-20-M	-6.39**	-0.88
CK 73 × CT 16346-CA-20-M	-2.32	1.86
Bonanca × CT 16350- CA-5-M	1.30	-1.74
WITA 2 × CT 16350- CA-5-M	7.12**	-1.63
CK 73 × CT 16350- CA-5-M	-3.17	2.26
Bonanca × CT 16344-CA-9-M	-10.27***	6.02**
WITA 2 × CT 16344-CA-9-M	4.24*	-3.67
CK 73 × CT 16344-CA-9-M	3.30***	1.12

** Significant at 0.01.

Significant at 0.001.

Table 7. Estimates of specific combining ability (SCA) effects for filled grains under drought and nondrought stress conditions.

3.2.5. Summary of analysis of generation of means

The mean, variance, and mean variance of filled grains for P1, P2, F1, F2, and F3 are shown in Table 8. The F2 populations had the highest variance followed by F3 and F1. Scaling tests for dominance × dominance and additive × additive interactions were nonsignificant for both levels. Dominance main effects were not significant, but additive main effects were significant at P = 0.01. When the mean scores were fitted to an additive model, it fitted with $r^2 = 0.77$ (Figure 3). Mean filled grains score was best linear unbiased estimator (BLUE) of the traits

The estimate of the number of genes that control filled grains trait based on Castle-Wrights method was 0.9 ≈ 1 gene. Estimate of the degree of dominance in the F1 and F2 generation based on the [15] method was $-3 \approx 0$ and $0.9 \approx 1$ level of dominance, respectively.

Descriptive summary of generations								
Generations	d.f	Mean	Variance	Mean variance				
P1	29	77.80	42.92	2.59				
P2	29	56.93	16.89	1.90				
F1	29	74.73	80.47	2.49				
F2	59	72.07	141.08	1.20				
F3	59	64.60	81.87	1.08				
Scaling test for filled	grains							
Interactions	Scale	SE	d.f	t (Scale/SE)				
dominance × dominance	-15	3.559	146	-1.184 ^{NS}				
additive × additive	3	3.361	176	-0.893 ^{NS}				
Components of mean	ns (three parameters)							
Gene effects	Expectation estimates	SE	t = (component/SE)	d.f				
Mean	57.0	1.176	48.46**	59				
Additive effects	10.5	0.707	14.85**	58				
Dominance effects	0.8	36.842	0.22	147				

Table 8. Summary of generations in variety 18 × 138 cross, scaling test, and components of means for filled grains score.

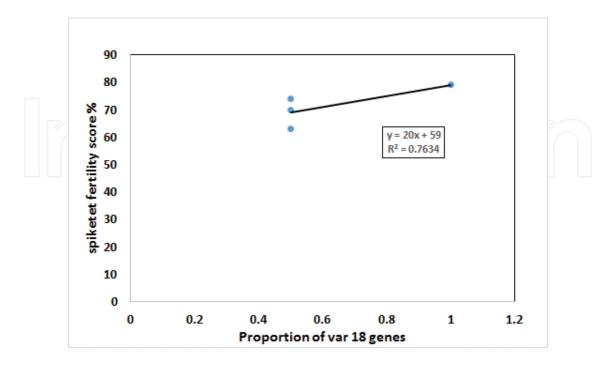


Figure 3. Proportions of genes contributing to filled grains score.

The narrow sense heritability in the generations from the cross between CT 16334 (2)-CA-2-M and WAB 450-1-BL1-136-HB using regression of F1 on mid-parents and F2 to F1 based on single seed decent are shown in **Figures 4** and **5** respectively. In the F1 to midparent regression, heritability of 60% was realized, but when F2 was regressed onto F1 means, the heritability estimate was 74%.

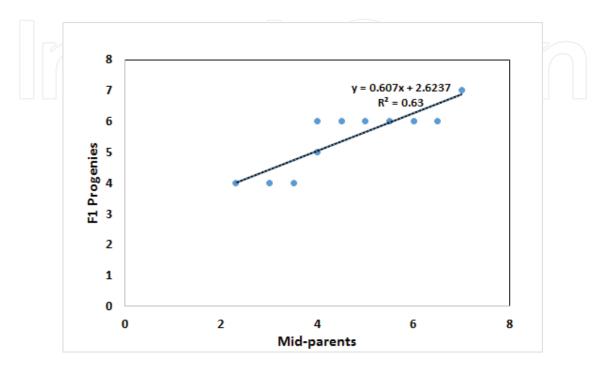


Figure 4. Regression of F1 progenies on midparents for 12 × 138 cross using filled grains.

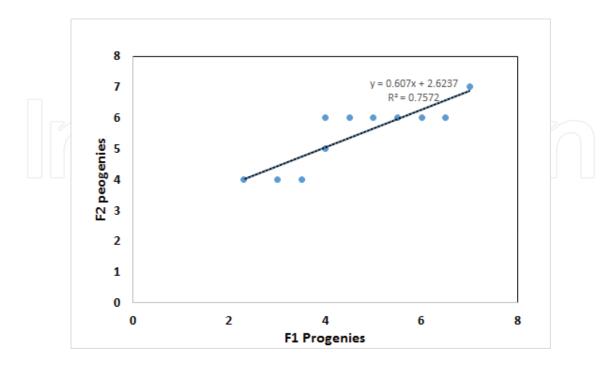


Figure 5. Regression of F2 progenies on F1 parental means for 12 × 138 cross using filled grains.

3.3. Evaluation of segregating lines

3.3.1. Preliminary evaluation of 660 F3

Results of evaluation of two sets of new 660 at NaCRRI are presented in this section. The first set grown under optimum moisture throughout the growth period is presented in **Table 9**. The selection pressure was 11.4% (75 out of 660 rows selected) for rain-fed lowland conditions and 9.85% (65 out of 660 rows selected) for rain-fed upland conditions. Candidate varieties CAIAPO/CT 16324-CA-9-M, WAB 450-1-BL1-136-B/WAB 450-B-136-HB, CT 16317-CA-4-M/WAB 365-B-1H1-HB, IRAT 325/WAB 450-B-136-HB, and CT 16342-CA-25-M/CK 73 are among the lines. Overall, 84 genotypes were selected for further evaluation.

Select	lection under rain-fed upland conditions			Selection under rain-fed lowland conditions			
No	Groups of crosses	Total	No	Groups of crosses	Total		
	One row crosses selected at F4			One row crosses selected at F4			
1	Bonanca × WAB 881-10-37-18-3-P1-HB		1	WAB 56-104 × CT 16324-CA-9-M			
2	IRAT 325 × WAB 450-B-136-HB		2	CT 16350- CA-5-M × WITA 2			
3	CT 16355-CA-15-M × IRAT 112		3	CT 16355-CA-15-M × IRAT 112			
4	WAB 365-B-1H1-HB × WAB 450-1-BL1-136-HB		4	CT 16317-CA-4-M × IRAT 104			
5	WAB 450-B-136-HB × IRAT 325		5	WAB 450-B-136-HB × IRAT 325			
6	CT 16344-CA-9-M × WITA 2		6	WAB 365-B-1H1-HB × IRAT 325			
7	WAB 365-B-1H1-HB × IRAT 325		7	CT 16313-CA-4-M × Caiapo			
8	WBK 35 (F3) × WAB 450-1-BL1-136-HB		8	WAB 56-104 × CT 16313-CA-4-M			
9	Bonanca × CT 16346-CA-20-M		9	CK 73 × CT 16346-CA-20-M	9		
10	CT 16342-CA-25-M × IRAT 257			Two rows crosses selected at F4			
11	WAB 450-B-136-HB × WAB 365-B-1H1-HB		1	IRAT 13 × CT 16342-CA-25-M			
12	CT 16334(2)-CA-2-M × IRAT 325		2	CT 16346-CA-20-M × Bonanca			
13	CT 16344-CA-9-M × CK 73		3	CT 16342-CA-25-M × CK 73			
14	CT 16344-CA-9-M × Bonanca		4	WAB 365-B-1H1-HB × IRAT 325	T		
15	Bonanca × WAB 450-I-B-P-38-HB	15	5	IRAT 112 × WAB 365-B-1H1-HB	10		
	Two rows crosses selected at F4			Three rows crosses selected at F4			
1	Caiapo × CT 16324-CA-9-M		1	Bonanca × WAB 881-10-37-18-3-P1-HB			
2	CT 16313-CA-4-M × WAB 56-104		2	WAB 365-B-1H1-HB × IRAT 325	6		
3	IRAT 325 × WAB 365-B-1H1-HB			Four rows crosses selected at F4			
4	CT 16324-CA-9-M × WAB 56-104		1	Caiapo × CT 16324-CA-9-M			
5	WAB 365-B-1H1-HB × IRAT 325		2	WAB 450-1-BL1-136-HB × WAB 450-B-136-HB			
6	WAB 450-B-136-HB × IRAT 112		3	CT 16324-CA-9-M × WAB 56-104	12		

Selec	tion under rain-fed upland conditions		Selec	tion under rain-fed lowland conditions	
No	Groups of crosses	Total	No	Groups of crosses	Total
	One row crosses selected at F4			One row crosses selected at F4	
7	CT 16334(2)-CA-2-M × IRAT 325	14		Five rows crosses selected at F4	
	Three rows crosses selected at F4		1	IRAT 325 × WAB 450-B-136-HB	5
1	WAB 450-1-BL1-136-HB × WAB 450-B-136-HB			Six row crosses selected at F4	
2	CT 16317-CA-4-M × WAB 365-B-1H1-HB		1	WAB 450-B-136-HB × WAB 365-B-1H1-HB	6
3	IRAT 112 × WAB 365-B-1H1-HB			Seven rows crosses selected at F4	
4	CT 16334(2)-CA-2-M × WAB 450-1-BL1-136-HB		1	WAB 365-B-1H1-HB × WAB 450-1-BL1-136-HB	
5	WAB 56-104 × CT 16313-CA-4-M		2	Bonanca × CT 16346-CA-20-M	14
6	CK 73 × CT 16350-CA-5-M			Thirteen rows crosses selected at F4	
7	IRAT 257 × CT 16355-CA-15-M	21	1	CT 16317-CA-4-M × WAB 365-B-1H1-HB	13
	Five rows crosses selected at F4				
1	IRAT 112 × WAB 450-B-136-HB				
2	IRAT 13 × CT 16342-CA-25-M				
3	CT 16342-CA-25-M × IRAT 13	15			
	Rows selected	65			75
	Total Hills planted	660			660
	Selection pressure	9.85			11.4

Table 9. Selection of F4 genotypes from 660 F3 genotypes.

3.3.2. Evaluation of 84 F4-F5 lines

Results of evaluation of 84 rain-fed segregating lines showed that 20 genotypes were resistant to RYMV, blast, and BLB in all the five locations, namely Namulonge, Kigumba, Kibaale, Lira, and Doho (**Table 10**). Results of yield in Lira are presented in **Table 11**. The best six genotypes in yield in descending order are P27-H14 (11,950 kg/ha), P29-H4 (9750 kg/ha), P36-H17 (9313 kg/ha), P5-H1 (9111 kg/ha), P36-H9 (8688 kg/ha), and P36-H4 (8417 kg/ha). When yield, pest and disease resistance, plant height, and panicle length was considered a total of nine lines were nominated for National Performance evaluation.

3.4. Evaluation of promising lines

Results of evaluation of nine selected lines along with two earlier selected lines and a local check is presented in **Table 12**. Six lines were selected and presented for release to the National Variety Release Committee of Uganda

No	Genotype	RYMV	Blast	BLB
1	P 22 H13 WAB 450-1-BL1-136-HB × WAB 450-B-136-HB	V	0	0
2	P 36 H1 WAB 365-B-1H1-HB × WAB 450-1-BL1-136-HB	0	0	0
3	16-16 CT 16344-CA-9-M × Bonanc	0	0	0
4	13-13 CT 16344-CA-9-M × CK 73	0	0	0
5	NERICA 4	0	0	0
6	P 25 H1 CT 16346-CA-20-M × Bonanca	0	0	0
7	P 8 H2 Caiapo × CT 16324-CA-9-M	0	0	0
8	77 WAB95-B-B-40-HB	0	0	0
9	96 WAB56-77	0	0	0
10	152 AB788-16-3-2-1-HB	0	0	0
11	P 24 H8 IRAT 13 × CT 16342-CA-25-M	0	0	0
12	P 1 H14 Bonanca × WAB 881-10-37-18-3-P1-HB	0	0	0
13	P 4 H6 CT 16350-CA-5-M × WITA 2	0	0	0
14	P 29 H1 CT 16342-CA-25-M × CK 73	0	0	0
15	P 23 H1 CT 16346-CA-20-M × WITA 2	0	0	0
16	P 45 H15 WAB 365-B-1H1-HB × IRAT 325	0	0	0
15	P 24 H9 IRAT 13 × CT 16342-CA-25-M	0	0	0
18	P 27 H10 CT 16317-CA-4-M × WAB 365-B-1H1-HB	0	0	0
19	P 5 H2 IRAT 325 × WAB 450-B-136-HB	0	0	0
20	P 29 H4 CT 16342-CA-25-M × CK 73	0	0	0

Table 10. List of 20 varieties that was resistant to RYMV, blast, and BLB in five locations: Namulonge, Kigumba, Kibaale, Lira, and Doho.

Seven genotypes namely 1. P5H2 (IRAT 325/WAB 450-B-136-HB-F6), 2. P29H4 (CT 16342-CA-25-M/CK 73-F6), 3. P8H2 (Caiapo/CT 16324-CA-9-M-F6), 4. ART3-11L1P1-B-B-2, ([WAB56-104 (WAB56-104/CG14)]/Moroberekan), 5. P27H1 (CT 16317-CA-4-M/WAB 365-B-1H1-HB-F6), 6. WAB 95 B-B-40-HB (ITA257/(IDSA6/ROK16)), and 7. P24H9 (IRAT 13/CT 16342-CA-25-M-F6), higher yields that NERICA-4 the local check. Under optimum conditions, six genotypes had higher yield than NERICA-4.

3.5. Varietal release and status of release

Breeding background, characteristics, and selected agronomic information on six varieties were presented to the variety release committee. These varieties were released based on important characteristics detailed in **Table 13**. The names proposed and accepted by the variety released committee were NamChe-1. NamChe-2, NamChe-3, NamChe-4, NamChe-5, and NamChe-6.

Rank	Acc no.	Yield	Rank	Acc no.	Yield	Rank	Acc no.	Yield	Rank	Acc no.	Yield
1	P27-H14	11,950	22	P35-H5	6625	43	P36-H16	6075	64	P22-H3	5156
2	P29-H4	9750	23	P59-H13	6625	44	P5-H14	6025	65	P55-H9	5139
3	P36-H17	9313	24	P59-H19	6625	45	P1-H14	6000	66	P27-H9	5100
4	P5-H11	9111	25	P27-H15	6550	46	P55-H2	5975	67	P27-H12	5071
5	P36-H9	8688	26	P36-H4	6500	47	P31-H3	5950	68	P28-H3	5025
6	P36-H4	8417	27	P55-H17	6500	48	P27-H10	5900	69	Р5-Н3	4825
7	P51-H17	8400	28	P5-H2	6500	49	P26-H17	5700	70	P8-H10	4594
8	P33-H3	7625	29	P50-H1	6469	50	P59-H9	5700	71	P26-H13	4500
9	P22-H6	7600	30	P1-H17	6400	51	P59-H8	5675	72	P7-H2	4300
10	P25-H14	7600	31	P22-H13	6375	52	P49-H3	5625	73	P45-H15	4275
11	P37-H13	7575	32	P59-H17	6375	53	P33-H6	5583	74	P24-H9	4250
12	P31-H15	7250	33	P26-H6	6350	54	P36-H1	5583	75	P27-H3	4179
13	P34-H2	7188	34	P27-H11	6350	55	P36-H8	5500	76	P8-H17	3700
14	P25-H1	7125	35	P38-H15	6325	56	P27-H1	5464	77	P55-H19	3650
15	P33-H1	7000	36	P7-H19	6325	57	P26-H18	5450	78	P1-H20	3500
16	P26-H1	6889	37	P55-H5	6275	58	P5-H4	5429	79	P4-H6	3400
17	P27-H18	6850	38	P22-H16	6250	59	P7-H14	5357	80	P27-H17	3300
18	P24-H8	6833	39	P59-H10	6214	60	P29-H1	5333	81	P59-H17	3125
19	P55-H10	6775	40	P35-H12	6188	61	P56-H19	5325	82	P27-H6	2800
20	P8-H2	6708	41	P55-H20	6125	62	P23-H1	5300	83	P27-H2	2679
21	P27-H7	6625	42	P58-H16	6083	63	P8-H15	5194	84	P58-H11	2607

NB: Yield of NERICA 4 was 5600 tons/ha

Table 11.	Yield of	f 84 bree	eding li	nes scree	ened at Lira.

Table 11.	rield of 8	34 breeding	lines screene	ed at Lira.					
Genotype	Arua	NaCRRI	Masindi	Soroti	Kibaale	Kanungu	Mean yield	Mean rank	Yield under optimal condition
1	2913	2653	2906	3464	2619	3284	2973	7.6	3500
2	2747	3026	3364	3703	2802	3673	3219	4.2	3600
3	4093	2954	3069	3984	3230	3561	3482	4.2	4300
4	2183	2538	2887	3196	2287	3187	2713	9.6	4500
5	3785	2351	2420	3454	2731	2949	2948	9.4	5800
6	3399	2364	2496	3369	2604	2974	2868	9.6	3800
7	4990	2214	2072	3651	3068	2773	3128	9.2	3750

Genotype	Arua	NaCRRI	Masindi	Soroti	Kibaale	Kanungu	Mean yield	Mean rank	Yield under optimal condition
8	2660	3086	3446	3726	2809	3737	3244	3.2	4013
9	4532	3235	3326	4305	3567	3837	3800	1.4	4550
10	4219	2937	3030	4003	3264	3540	3499	4.4	3650
11	3656	3023	3218	3928	3121	3644	3432	4	3600
12	3928	2080	2084	3286	2606	2666	2775	11.2	3780
2. P29H4 (0 3. P8H2 (C	CT 16342 aiapo/C	2-CA-25-М/0 Г 16324-CA-			514)]/Moro	berekan).	P		

5. P27H1 (CT 16317-CA-4-M/WAB 365-B-1H1-HB-F6).

6. WAB 95 B-B-40-HB (ITA257/(IDSA6/ROK16)).

7. P24H9 (IRAT 13/CT 16342-CA-25-M-F6).

8. NERICA-4.

9. P29H1 (CT 16342-CA-25-M × CK 73–F6).

10. P23H1 (CT 16346-CA-20-M/WITA 2-F6).

11. ART8-L15P14-1-2-1.

12. P22 H13 (WAB 450-1-BL1-136-HB/WAB 450-B-136-HB-F6).

Table 12. Yield of 12 genotypes in six locations in the country and under optimal conditions.

Variety name	NamChe 1	NamChe 2	NamChe 3	NamChe 4	NamChe 5	NamChe 6
Year of release	2013	2013	2013	2013	2013	2013
Local name	NamChe 1	NamChe 2	NamChe 3	NamChe 4	NamChe 5	NamChe 6
Pedigree	WAB95-B- B-40-HB	NM7-8-2- B-P-11-6	NM7-29-4- B-P-80-8	ART3-11L1P1- B-B-2	NM7-27-1-B- P-77-6	NM7-5-2-B-P-79-7
Parents	ITA257/(IDSA6/ ROK16)	Caiapo/ CT 16324- CA-9- M-F6[25]	CT 16342-CA- 25-M/CK 73	[WAB56-104/ (WAB56-104/ CG14)]/ Moroberekan	CT 16317- CA-4-M/WAB 365-B-1H1-HB	IRAT 325/WAB 450-B-136-HB–
Test names	WAB95-40	NM7-1	NM7-8	ART3-10	NM7-6	NM7-7
Breeding center	AfricaRice, Senegal	NaCRRI, Uganda	NaCRRI, Uganda	AfricaRice, Ibadan	NaCRRI, Uganda	NaCRRI, Uganda
Characteristics						
Leaf planotype	Semi-erect	Semi-erect	Erect	Erect	Semi-erect	Erect
Culm inclination	Semi-erect	Semi-erect	Erect	Erect	Erect	Erect
Culm length (cm)	64	66	66	65	60	62
Duration from germination to harvest (days)	110	132	125	120	125	125

Variety name	NamChe 1	NamChe 2	NamChe 3	NamChe 4	NamChe 5	NamChe 6
Year of release	2013	2013	2013	2013	2013	2013
Milling percentage	66.2	68.7	72.7	72.1	71.4	70.4
Volume expansion	1.7	1.6	1.6	1.9	2	1.9
Yield (kg/ha)	3800	4300	4550	4500	5800	5000
1000 grain weight (g)	29	28	24	27	26	23
Grain length dehusked (mm)	6.3	6.7	6.3	6.5	6.4	6.4
Grain width dehusked (mm)	2.4	2.2	2.2	2.1	2.2	2.2

Table 13. Major characteristics of the released varieties.

4. Discussions

4.1. Screening introductions for drought tolerance

Results that nine out of 20 best lines were from the CT breeding work imply there was adequate variability in the selected set for selection of suitable genotypes. There were five out of 20 genotypes also indentified as drought tolerant. Also, result that three reference genotypes namely NERICA 7, CO 39, and VANDANA were suitable for identified as drought tolerant in this study implies that the method of screening was acceptable.

4.2. Genetic analysis for filled grains and other agronomic traits

The analysis of F2 crosses revealed the various components of gene action controlling various drought tolerance traits in rice. Both male GCA and female GCA effects were significant for filled grains under both DS and NDS, for the A populations and the B populations under DS. The finding that the additive effects were more important than nonadditive effects for total number of grains filled, grains in set A under NDS and B under NDS and DS, implies that additive effects control the traits in different populations and the nonadditive effects varied with populations under study. This result is contrary to the finding by Mohapatra and Mohanty [16] that filled grains was predominantly controlled by nonadditive gene effects under drought stress. However, in the study by Mohapatra and Mohanty [16], the populations were generated by crossing O. sativa with O. sativa. The mechanism of drought tolerance in O. glaberrima, a parent of the interspecific rice used in the current study, was reported to be different from that of O. sativa [17]. This could explain the apparent differences in findings of the current study when compared with that of Ref. [16]. Based on the current study, breeding methods that involve selection in the early generations are recommended. The methods include single seed decent, pedigree selection, and modified bulk methods. Studies using more populations generated from O. sativa and interspecific rice could confirm our finding that the importance of SCA varies with population under study.

Findings of this study that nonadditive effects for total number of grains per panicle was important in both set A and set B under NDS conditions, implies that breeding methods that involve late selection could improve drought tolerance under NDS using number of grains per panicle trait. The use of yield components including grains per panicle has been demonstrated to be effective in improving yield under drought stress by selecting under NDS conditions [18]. The differences between the responses under DS and NDS conditions for total number of grains per panicle could be due to fewer loci within the set B that could segregate for the trait than in A. Set B comprised of lines with more susceptibility to drought stress than those in set A.

Additive effects for number of grains per panicle were important in all the population in set A and set B, under DS and NDS. This implies that breeding methods that involve selection in the early generations especially, single seed decent, pedigree selection, and modified bulk methods could improve drought tolerance through selection of number of grains per panicle. In another study involving *O. sativa* parents that included susceptible, moderately susceptible, moderately resistant and resistant lines, number of grains per panicle was reported to be controlled by additive effects under NDS conditions [19]. Genes with additive effects were predominant in the inheritance of number of grains per panicle [16]. Both additive and nonadditive effects were nearly equal in populations in set A, under NDS. These set of populations could be used to improve drought stress using methods that involve selection in the early and late generations of the populations. These methods include modified bulk methods and repeated crossing at the segregation stage. Similarly, additive and nonadditive gene effects were significant for number of spikelets per panicle under both normal and saline conditions, and repeated crossing has successfully been used to improve salinity tolerance [20].

Findings of this study that nonadditive effects for leaf area were more important than additive effects in both set A and set B under DS conditions, suggests that late selection could improve drought tolerance. In addition, the findings that additive effects were more important than nonadditive effects for the populations in sets A and B under NDS implied that selection methods that involve early selection could be employed under NDS. In the populations in sets A and B, interspecific rice genotypes generated from *O. glaberrima* crosses were the majority of the parents. *O. glaberrima* is known to have high vegetative growth as a drought stress adaptation mechanisms [21, 17]. It is likely that these traits were transmitted to the populations under study and it is expressed more under DS than under NDS conditions.

Results of this study that additive and nonadditive effects for plant height were nearly equal with contribution for total GCA, varying between 45 and 55% for both set A and set B under DS and NDS conditions, implied that that breeding methods that involve both early and late selection could be employed in the improvement of drought tolerance using this trait. Modified bulk method of selection method could be appropriate. In another study involving *O. sativa* parents that included susceptible, moderately susceptible, moderately resistant and resistant lines, and plant height was controlled by additive effects under NDS conditions [19]. In the current study, both additive and nonadditive effects were important when the B generations were tested under DS and NDS conditions. Drought traits were controlled quantitatively.

The current study found that additive effects were the more important in the transmission of drought tolerance using tiller number as evidenced by the lack of significance for male × female interaction effects for tiller number. This finding is contrary to the work reported by other scientists that nonadditive effects were more important under drought stress conditions [22, 23]. In another study, however, expression of tiller number, under both NDS and DS situations, was found to involve nonallelic gene interactions [20].

Overall, in situations where nonadditive effects are more important, selection should be delayed until later generations. In these types of populations, repeated crossing in the segregating generations may be useful to pool all the desirable genes in one genotypes according to Ref. [24]. The modified bulk method is another useful method of improvement. However, when additive affects are more important, then a modified pedigree method that involves bulking germplasm before evaluation is appropriate. However, when both additive and non-additive effects are important, two options can be taken depending on the objective of the breeding and the relative importance of the additive or nonadditive effects. In case, if the objective is to develop hybrid rice, as it is planned in Uganda, then pure line selection should be employed. In this approach, additive effects will be extracted because rice is autogamous [25]. In a situation, where both additive and nonadditive gene action are to be exploited, a modified bulk breeding method would hasten the rate of genetic improvement. Similar exploitation of both additive and nonadditive gene action has been conducted in the improvement of cold tolerance [26] and sodicity tolerance in rice [27].

4.3. Combining abilities filled grains under drought stress

Generally, there was no clear distinction in combining ability between *O. sativa* and interspecific rice lines under nondrought stress conditions, but the interspecific lines were better combiners under drought stress conditions. Among the *O. sativa* line, IRAT 325 was a good general combiner, while CT 16350-CA-5-M and WAB 450-B-136-HB (NERICA 9) were good combiners under nondrought stress conditions. In the drought stress condition, however, CK 73, an *O. sativa* genotype, was the best combiner for improved filled grains. Other parents with lower levels of significance were CT 16344-CA-9-M, WAB 450-B-136-HB (NERICA 9), and CT 16346-CA-20-M.

Specific combining ability analysis revealed that crosses WITA 1 × CT 16350-CA-5-M, Bonanca × CT 16346-CA-20-M, and CK 73 × CT 16344-CA-9-M were best under NDS condition. The cross CK 73 × CT 16344-CA-9-M had both parents as good combiners indicating additive × additive type of gene action. It is expected that these crosses could provide transgressive segregants that could be selected using pedigree methods [28]. The others crosses had mixed combiners, therefore additive and nonadditive gene action could be the major contributors. In such crosses, bulk breeding methods could exploit both gene actions.

4.4. Generation means for filled grains under drought stress

There were significant differences among generations for filled grains indicating the presence of sufficient genetic variability. Variability for various traits of rice has been reported [29–32]. The scaling test showed that additive genetic effects but not dominance and epistatic genetic

effects were important in the inheritance of filled grains. Fitting means of filled grains on the additive model showed that additive effects accounted for 77% of the genetic variation. In addition, the finding that dominance level was 0 in the F1 population showed that there were no dominance effects.

The generation means analysis confirmed that additive effects were significant in the transmission of filled grains in the populations generated. This study had no inconsistencies in detecting that additive effects were the most important genetic factor in the population under study. In addition, results where narrow sense heritability was high indicated that a high proportion of genetic components of variance can be fixed in segregating generations. Since the selection was conducted under drought stress, it is appropriate that selection for improved drought stress is conducted as early as F2 in the study location. According to Ref. [31], it is appropriate that selection for improved drought stress is conducted using heritability estimates for target traits. There is limited information on the inheritance of filled grains trait under drought stress. However, various reports indicated that additive effects were the main components that controlled the transmission of this trait under high temperature [33, 34]. A single gene pair was estimated to control filled grains under drought stress. A single gene was found to be responsible for the transmission of filled grains under high temperatures [33, 34].

4.5. Evaluation of segregating lines

Results of evaluation of two sets of new 660 genotypes showed that CT lines namely CAIAPO, CT 16324-CA-9- CT 16317-CA-4-M and CT 16342-CA-25-M had the highest number of parents that could improve the landraces. These lines were developed for drought tolerance through CIAT Colombia Breeding program.

Results of evaluation of 84 rain-fed genotypes that P27-H14 P29-H4 P36-H17, P5-H1 P36-H9 and P36-H4 were the preferred genotypes based on resistance to diseases and yield concurs with other reports (3, 23) that rice varieties with tropical Japonica have higher resistance to RYMV and other diseases.

4.6. Evaluation of promising lines

Results of evaluation of nine selected lines along with two earlier selected lines and a local check is presented in **Table 12**. Although seven varieties were more had higher yields than NERICA-4, only six were presented for release when information on milling and cooking qualities were considered. These genotypes were: **1**. P5H2 (IRAT 325/WAB 450-B-136-HB-F6), **2**. P29H4 (CT 16342-CA-25-M/CK 73-F6), **3**. P8H2 (Caiapo/CT 16324-CA-9-M-F6), **4**. ART3-11L1P1-B-B-2, ([WAB56-104/(WAB56-104/CG14)]/Moroberekan), **5**. P27H1 (CT 16317-CA-4-M/WAB 365-B-1H1-HB-F6), and **6**. WAB 95 B-B-40-HB (ITA257/(IDSA6/ROK16).

4.7. Varietal release and status of release

Breeding background, characteristics, and selected agronomic information on six varieties were presented to the variety release committee. These varieties were released based on important characteristics summarized in Table 13. Information from genetic studies during F2 generation guided selection of promising lines from F2 through F6. Subsequently, promising varieties were nominated for National Performance Trials and eventually released. Four new varieties were released namely, NM7-8-2-B-P-11-6 generated from CAIAPO/CT 16324-CA-9-M cross, NM7-29-4-B-P-80-8 (CT 16342-CA-25-M/CK 73), NM7-5-2- B-P-79-7 (IRAT 325/WAB 450-B-136-HB), NM7-27-1- B-P-77-6 (CT 16317-CA-4-M/WAB 365-B-1H1-HB), and NM7-5-2- B-P-79-7 (IRAT 325/WAB 450-B-136-HB). These varieties were assigned release names, where WAB95-B-B-40-HB was named NamChe-1 at the release in Uganda and ARICA 5 by the AfricaRice Breeding Task Force. ARICA acronym means advanced rice for Africa, implying that the harmonized names are to be used by all parties involved. Another variety bred by AfricaRice is NamChe-1 (ARICA-5) with designation ART3-11L1P1-B-B-2. Of the six varieties released, four were bred from Uganda with support from Alliance for Green Revolution in Africa (AGRA) and the other two were developed by AfricaRice through the AfricaWide Rice Breeding Task Force with support from Stress-tolerant rice for poor farmers in Africa and South Asia. These were NamChe-2 (NM7-8-2-B-P-11-6), NamChe 3 (NM7-29-4-B-P-80-8), NamChe 5 (NM7-27-1- B-P-77-6), and NamChe 6 (NM7-5-2- B-P-79-7). The acronym NamChe means Namulonge Mchere (Mchere means uncooked rice in Kiswhili rice). In 2015, over 20,000 ha was under production based on figures of direct seed sale by different producers.

5. Conclusion

This research found that there was adequate variability in the rice population studied for secondary traits for drought tolerance namely, leaf roll and filled grains. However, the filled grains were found to be more informative and therefore recommended for further studies. Of the three rice groups *O. sativa*, interspecific lines, and *O. glaberrima*, there was high similarity between *O. sativa* and interspecific lines. This similarity could make crossing easy.

The genetic studies for drought provided information on the gene action for drought tolerance at reproductive stage of crosses between interspecific and *O. sativa* genotypes. Evidence of additive, nonadditive, additive × additive, and dominance effects were found for drought stress at reproductive stage. Additive effects were the most important components that controlled filled grains in most of the populations. This suggests that breeding methods that involve selection in the early generation could therefore be helpful in improving rice for filled grains. These methods include pedigree breeding, pure line selection, mass selection, single seed decent and progeny selection. In a few crosses, however, proportion of filled grains was controlled by nonadditive effects. Methods that involve a delay in selection of genotypes would be appropriate for improving filled grains in these populations. Modified bulk methods of selection are proposed to be employed in this breeding. Tests for magnitude of the gene action for filled grains using additive-dominance model confirmed that additive gene effects were the most important and additive × additive, as well as, additive × dominance effects were not important. Genotypes *O. sativa*, namely WITA 1 (*O. sativa* indica), IRAT 325 (*O. sativa* japonica), CT 16350-CA-5-M (*O. sativa* japonica), and WAB 450-B-136-HB (NERICA 9) (interspecific) were good combiners under nondrought stress condition for filled grains. In the drought stress condition, however, CK 73, an *O. sativa* genotype, was the best combiner for improved filled grains. Specific combining ability analysis revealed that crosses WITA 2 × CT 16350- CA-5-M, Bonanca × CT 16346-CA-20-M, WITA 2 and CT 16344-CA-9-M were best under NDS condition.

Follow up of their performance in countries in the region shows that NamChe-3 (NM7-29-4-B-P-80-8) and NamChe-2 (NM7-8-2-B-P-11-6) could be mega variety and a major source of disease resistance. In 2015, over 20,000 ha was under production based on figures of direct seed sale by different producers. This is a success story demonstrating the benefit of collaboration and rigorous breeding in the development of locally adapted rice varieties.

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