



Estimation of Combining Abilities for Grain Yield of Tropical and Exotic Maize Inbred Lines in Diverse Environments

*Ogunniyan, D.J., Anjorin, F.B. and Akintunde, A.T.

Institute of Agricultural Research and Training, Obafemi Awolowo University, Moor Plantation, Ibadan, Nigeria.

*Author for correspondence. E-mail: dotunogunniyan@yahoo.com

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Abstract

Studies on the combining ability of maize inbred lines have enhanced the effective selection of parents of promising hybrids for specific or across agro-ecologies. Exotic lines have been reported to provide novel genes for maize improvement. This trial, therefore, estimated the combining abilities for grain yield of local and exotic inbred lines of two types of maize. One hundred and fifty white and 66 yellow hybrid maize were evaluated in three locations in the rainforest, derived savannah, and savannah agro-ecologies of Nigeria for two years. The layout for the white maize was a 19 x 8-lattice design, while a 10 x 7-lattice design was used for the yellow maize, with three replicates each. Estimated grain yields were pooled and analyzed for each location and across locations. Mean squares due to environments, genotypes, genotype-environment interactions, and male x female interactions were significant in all locations and across locations. Three inbred lines, BD74-171, BD74-179, and BD74-170, had significant positive general combining ability (GCA) across locations for the white maize, while TZEI12, TZEI16, BD74-161, and BD74-222 were identified as good general combiners for the yellow maize. Hence, the respective lines can be tracked for the improvement of white and yellow hybrids adapted to the locations. White hybrids BD74-175 x BD74-147, BD74-170 x TZEI106, and TZEI4 x BD74-152 and six yellow hybrids had significant positive specific combining ability (SCA) across locations. They are recommended for further research in the agro-ecologies. Higher SCA over GCA in grain yield indicates the predominance of non-additive gene effects controlling the inheritance of grain yield in the two types of maize in the locations.

Introduction

Maize (*Zea mays* L.) is the third most important cereal crop in the world that is used as food, feed and raw materials for industries in Africa and humid tropics (Grote et al., 2021; Erenstein et al., 2022). Compared to wheat and rice, maize is a more versatile multi-purpose crop. It also provides employment and generates earnings for small-holder households (Mwimali et al., 2015; Erenstein et al., 2022). The crop is cultivated during the rainy and dry seasons in West and Central Africa. However, the grain yield of maize in the tropics is still lower than what is obtainable in the temperate region. It is about 2 t ha⁻¹ in Africa as against about 8 t ha⁻¹ in temperate countries (FAOSTAT, 2021). Plant breeders and other scientists have adopted several methods to improve the grain yield of maize in sub-Saharan Africa (SSA). Among the efforts were improved agronomic practices and

extensive exploitation of heterosis. Yet, the expected result has not been achieved.

Effective choice of parents for crosses through combining ability is a necessity for efficient and successful maize breeding (Mwimali et al., 2015). Ability of parent lines to hybridize among themselves and transmit traits of interest to their resultant progenies is important in maize improvement. The proficiency can be determined by the estimation of combining abilities of the parent lines. There are two types of combining abilities. General Combining Ability (GCA) is described by Sprague and Tatum (1942) as the average performance of a genotype in a series of hybrid combinations. Specific Combining Ability (SCA) describes the expected performance of a particular hybrid combination. The individual and combined effects of GCA and SCA are important indicators of the potential value of inbred lines in hybrid combinations. They give

information on gene actions in the expression of superior performances as well as improving the efficiency of selection for promising hybrids in breeding programmes. The concept has largely been deployed for maize improvement (Adebayo et al., 2014; Badu-Apraku et al., 2016; Ali et al., 2018; Ogunniyan et al., 2019a). However, it is gradually being employed by plant breeders for other crops because hybrid varieties are now more widely used by farmers (Ishaq and Raziuddin, 2016; Ingle et al., 2018; Kargbo et al., 2019).

Distinction of GCA and SCA may occur as a result of the difference in the allele frequencies of the tester (Hallauer et al., 2010). Crop performance can be better or poorer than expected on the basis of the average performance of the parental inbred lines. The GCA is usually attributed to genes that are largely additive while SCA is due to those that exhibit dominant or epistatic effect (Kamara et al., 2014). High GCA estimate indicates less effects of the environment on the performance of crops. It may also suggest the superiority or inferiority of the mean value for the parents to the general mean (Chigeza et al., 2014). On the other hand, low GCA estimates stipulate the presence of little variation between the mean of parents in crossing and general mean of the crosses. This guarantees strong transference of the desirable gene from parents to offspring and shows predominance of additive genes in the inheritance of the trait (Franco et al., 2001).

Many years of intensive cultivation of land had made low soil nitrogen (low N) significant among the abiotic factors that limit cereal production and productivity, especially maize in SSA (Sanchez, 2010; Ismaila et al., 2010; CTA, 2015). The estimated annual loss of maize yield due to low N stress varies from 10 to 80% (Badu-Apraku et al., 2010; 2011; 2013; Obeng-Bio et al., 2019; Ertiro et al., 2020). Fertilizer use in SSA is minimal due to its scarcity and high cost, therefore genetic approaches to maintaining the grain yield of maize at reduced rates of N with its attendant negligible damage to the environment are highly essential. Estimates of GCA and SCA have been used in several studies to detect the gene actions involved in various cross combinations of maize inbred lines. Published reports are, however, not consistent on the gene actions controlling grain

yield and low N tolerance of maize inbred lines. Factors responsible for the contradictory reports on the combining abilities of maize inbred lines under various N conditions are linked to the variations in the source germplasm from which the inbred lines were derived (Makinde et al., 2023).

It has been reported that additive, non-additive or both additive and non-additive gene actions were responsible for the inheritance of grain yield of maize under various levels of soil N (Ige et al., 2017; Annor et al., 2019; Ogunniyan et al., 2019a). Some studies have reported that the non-additive gene actions-controlled grain yield under low N while additive gene actions-controlled grain yield under high N (Makumbi et al., 2011; Makinde et al., 2023). On the other hands, some have reported additive gene actions to be preponderant for the inheritance of grain yield under low N while non-additive gene actions conditioned yield under high N (Kearsey and Pooni, 1996;). Therefore, this study aimed at estimating the combining abilities of white and yellow endosperm maize with a view of understanding the gene actions responsible for the expression of grain yield under low nitrogen in diverse climatic conditions.

Material and Methods

Description of experimental fields

The experimental locations were Kisi [03.51° E and 9.05° N 364 m above sea level (asl); Ibadan (3.56° E and 7.33° N 168 m asl) and Iwo (04.18° E and 07.63° N 231m asl). Kisi lies in Guinea Savanna; Ibadan in Rainforest-Savanna-Transition and Iwo in Derived Savanna agro-ecologies. The experimental plot was depleted of its native N by continuously planting maize at a very high population density on the soil without fertilizer. The biomass was uprooted and removed completely from the field after each cropping. This depletion exercise was repeated until the soil N was completely removed. Soil analysis was carried out to confirm the N status after each depletion process.

Evaluation of the hybrids

One hundred and fifty white hybrids and 66 yellow hybrid maize were evaluated with their respective parents in nitrogen (N) depleted soil at three different locations in 2014 and 2015.

The 150 white hybrids were generated from 20 inbred lines using North Carolina Design II mating design while 12 yellow inbred lines were crossed in a non-reciprocal diallel mating system (Griffing, 1956) to generate 66 yellow hybrid maize. Two and four checks were evaluated along with the white and yellow hybrids, respectively.

The experiment for evaluating the white kernel hybrid maize was laid out in 19×8 lattice design while layout for the yellow kernel hybrids was 10×7 lattice design with three replicates each. Plot was a single row of 4.8 m long and 0.75 m apart, where plants were spaced 0.4 m within a row. Three seeds were sown and later thinned to two stands per hill at two weeks after planting (WAP) to attain plant population density of 66,666 plants ha^{-1} . Fertilizer was applied in the form of N: P: K 15:15:15 at 30 kg ha^{-1} to each of plots at 4 WAP. All the plots received 30 kg P ha^{-1} as single super phosphate (P_2O_5) and 30 kg K ha^{-1} as muriate of potash (K_2O). Standard cultural practices for field maintenance were applied according to the recommendation of IAR&T (2010). Data were collected on the grain weight and moisture content at harvest. The parameters were used to estimate the grain yield per ha adjusted to 15% moisture content according to CIMMYT (1985):

$$\frac{\text{GW (kg)}}{7.5\text{m}^2} \times \frac{100-\text{MC}}{100-15\%} \times 10,000 \text{ m}^2$$

where, GW = Grain weight, MC = grain moisture content at harvest, storage moisture content = 15%, plot area = 10 m^2 and $1 \text{ ha} = 10,000 \text{ m}^2$.

Data analysis

The grain yield data were pooled and subjected to combined analysis of variance using SAS (2009) separately for each location, and across locations for the two years. The main effects due to males and females were independent estimates of GCA while effects due to male \times female were the SCA. The GCA effects of female and male parents were tested for significance using their interactions as the error variance. The SCA effects were tested for significance using the error variance while environmental interaction was tested against the error pooled across environments according to Dhliwayo et al. (2009). In the ANOVA

performed on the data for the 66 yellow kernel hybrids, effects of GCA of the parents and SCA of the hybrids were estimated from their mean square values adjusted for block effects for individual and across with DIALLEL SAS programme developed by Zhang et al. (2005) adapted to SAS software (SAS, 2009).

The cross sums of squares were partitioned to determine the relative contributions of female and male GCA effects as:

$$\frac{\sigma^2\text{GCA}}{\sigma^2\text{GCA} + \sigma^2\text{SCA}}$$

where $\sigma^2\text{GCA}$ and $\sigma^2\text{SCA}$ are the variance components for GCA and SCA. The closer the ratio is to 1, the higher the probability that progeny performance can be adequately predicted from GCA. The closer this ratio is to zero, the greater the importance of SCA in predicting progeny performance. High GCA strength implies that additive genetic effects are more important for the inheritance of the yield, while non-additive genetic effects were more important for the trait when SCA effects are predominant (Hung and Holland, 2012).

Results

Mean squares for grain yield of the maize in diverse locations

Mean squares of genotypes (G), genotype \times environment ($G \times E$), female (F) and female \times male ($F \times M$) were highly significant ($p \leq 0.01$) in Kisi and Ibadan (Table 1). There was a slight difference in the levels of significance at Ibadan where effect of male was significant at $p \leq 0.05$ for the yellow maize. Results across locations showed significant effects of environment, genotype, $G \times E$, female, male, and female \times male. Effects of interactions of the environments and the parents; namely $E \times F$ and $E \times M$ were not significant for the grain yield in all the locations, and across locations.

Estimates of combining ability for grain yield of the maize inbred lines at the three locations

GCAs for the white inbred lines: Positive and negative estimates of GCA were observed in all the locations and across locations (Table 2). Inbred lines BD74-128, BD74-171, BD74-55, BD74-31 and BD74-170 had significant positive GCA while lines TZEI2, TZEI36 and TZEI1

Table 1. Mean squares for grain yield from the analysis of variance for the white and yellow hybrid maize evaluated at Kisi, Ibadan and Iwo, Nigeria in 2014 and 2015

Source of variation	White endosperm maize		Yellow endosperm maize	
	df	Mean square	df	Mean square
Kisi				
Environment (Env.)	1	68053.0***	1	44501.3*
Block (Env. × replicate)	108	728.5*	36	200.6 ^{ns}
Genotype	151	6662.8***	69	4763.3***
Genotype × Env.	151	2247.8***	69	1873.4***
Female	24	6868.1***	10	9027.9***
Male	24	8012.3**	10	3574.4***
Female × Male	96	4442.0**	45	6552.7***
Env. × Female	24	2197.0 ^{ns}	10	927.2 ^{ns}
Env. × Male	24	963.7 ^{ns}	10	1180.0 ^{ns}
Env. × Female × Male	96	2398.3***	45	1112.9***
Pooled error	488	529.8	224	278.4
Ibadan				
Environment (Env.)	1	16760.3*	1	23322.1***
Block (Env. × replicate)	108	284.7 ^{ns}	36	120.5 ^{ns}
Genotype	151	2825.0***	69	1047.4***
Genotype × Env.	151	1063.1***	69	1146.5***
Female	24	2218.6**	10	7662.2**
Male	24	2689.3**	10	2802.3*
Female × Male	96	1851.2**	45	2020.1***
Env. × Female	24	811.9 ^{ns}	10	1208.4 ^{ns}
Env. × Male	24	1270.8 ^{ns}	10	824.3 ^{ns}
Env. × Female × Male	96	1077.4 ^{ns}	45	553.0
Pooled error	488	283.2	224	102.9
Iwo				
Environment (Env.)	1	297049.8***	1	72415.1*
Block (Env. × replicate)	108	1732.4 ^{ns}	36	176.7 ^{ns}
Genotype	151	5279.2***	69	932.3***
Genotype × Env.	151	2862.7***	69	623.3***
Female	24	4916.8*	10	311.6*
Male	24	7171.9*	10	2818.0**
Female × Male	96	4304.0**	45	2209.0*
Env. × Female	24	23289 ^{ns}	10	151.7 ^{ns}
Env. × Male	24	3402.1 ^{ns}	10	387.0 ^{ns}
Env. × Female × Male	96	2865.1***	45	424.4 ^{ns}
Pooled error	488	1689.6	224	199.4
Across locations				
Environment (Env.)	5	117792.5***	5	44429.9***
Block (Env. × replicate)	324	915.2 ^{ns}	108	165.9.0 ^{ns}
Genotype	151	6181.6***	69	4009.1***
Genotype × Env.	755	2951.8***	345	1275.5***
Female	24	5443.2**	10	13442.9***
Male	24	6965.8**	10	5568.8***
Female × Male	96	3356.4**	45	5461.5***
Env. × Female	120	2779.6 ^{ns}	50	1717.8 ^{ns}
Env. × Male	120	3308.8 ^{ns}	50	1089.0 ^{ns}
Env. × Female × Male	480	2716.3	225	1248.3***
Pooled error	1464	834.2	672	193.6

*, **, *** and df mean significant at 5%, 1%, 0.1% and degree of freedom respectively

had negative significant GCA in Kisi. Four inbred lines namely TZEI7, BD74-179, BD74-174 and BD74-399 had significant positive GCA while TZEI106, BD74-152 and BD74-170 had negative significant GCA in Iwo. Results further showed that lines BD74-171, BD74-179 and BD74-170 had significant positive GCA effects in Ibadan, while the effects of GCA of lines BD74-171, BD74-55 and BD74-179 were positive across the three locations.

GCAs for the yellow inbred lines: At least five yellow inbred lines had significant GCA effects in each of the locations and across locations (Table 3). Only two inbred lines (TZEI8 and TZEI16) had significant positive GCA while three inbred lines (TZEI13, TZEI12 and TZEI11) had negative significant GCA in Kisi. Inbred lines, BD74-165, BD74-161 and BD74-222 had significant positive effects in Ibadan while TZEI11 and TZEI124 had negative significant GCA in the location. The significance of GCA of TZEI13 and TZEI12 were positive and those of TZEI10, TZEI128

and TZEI1 were negative in Iwo. The GCA of the yellow maize across locations however, were TZEI12 (346.2*), TZEI11 (-787.6*), TZEI16 (184.6*), BD74-161 (170.1*) and BD74-222 (176.9*).

SCAs for white hybrid maize: Out of the 39 hybrids that had significant positive SCA in at least one location, 17, 14 and 10 hybrids had significant SCA at Kisi, Ibadan and Iwo, respectively (Table 4). Only two hybrids namely TZEI4×BD74-152 and BD74-175×BD74-147 had significant SCA across the locations. Hybrid BD74-170×TZEI106 had significant positive SCA at both Kisi and Ibadan while hybrid TZEI4×BD74-152 had significant positive SCA at Kisi and across locations. However, the SCA effect of BD74-175×BD74-147 was significantly positive at Ibadan, Iwo and across locations. Of the hybrids that had significant positive SCA in at least one location, 71% were in Kisi and 50% each in Iwo, Ibadan and across locations were from crosses between IITA and CIMMYT lines.

Table 2. Estimates of GCA for grain yield of 20 white inbred lines evaluated in hybrids at Kisi, Ibadan, Iwo and across locations in Nigeria in 2014 and 2015

Inbred line	Kisi	Ibadan	Iwo	Across locations
TZEI106	102.2	-219.2	-612.4*	-243.1
TZEI2	-574.1*	-186.0	94.4	-221.6
BD74-128	325.2*	170.1	-27.5	155.9
TZEI136	-986.1*	-644.5*	-163.4	-598.0*
TZEI1	-881.5*	-457.8*	-278.3	-539.2*
BD74-152	-516.8	241.3	-833.0*	-369.5*
BD74-171	1117.7*	521.9*	-94.9	514.9*
TZEI98	-145.7	-25.8	61.8	-36.6
TZEI188	-149.7	161.7	268.4	93.5
TZEI4	-206.4	-75.6	-21.4	-101.1
BD74-55	748.1*	173.6	171.8	364.5*
BD74-147	282.1	60.0	-336.6	1.9
TZEI7	-86.5	-19.4	735.0*	209.7
BD74-31	529.4*	225.2	-63.8	230.3
BD74-179	272.2	412.3*	606.6*	430.4*
TZEI3	-271.1	-343.8*	190.1	-141.6
TZEI22	-246.9	-168.9	241.6	-58.1
BD74-170	308.2*	497.0*	-427.5*	125.9
BD74-175	152.6	-644.3	1172.9*	227.1
BD74-399	-47.5	302.1	692.6*	315.8

* means significant effects

Table 3. General combining ability for grain yield of the yellow maize inbred lines evaluated at Kisi, Ibadan, Iwo and across locations in 2014 and 2015

Inbred line	Kisi	Ibadan	Iwo	Across
TZEI13	-356.1*	90.4	107.8*	-52.6
TZEI146	-183.9	37.4	138.7*	-2.6
TZEI10	-60.4	-111.7	-205.8*	-126.0
TZEI12	-671.3*	140.8	226.4*	346.2*
TZEI128	116.8	14.0	-162.7*	-10.6
TZEI11	-799.9*	-1001.0*	-561.4*	-787.6*
TZEI8	233.7*	-89.4	36.3	60.2
TZEI16	365.9*	124.2	63.7	184.6*
TZEI124	-17.1	-222.1*	-11.9	-83.7
BD74-165	120.9	327.1*	-72.7	125.1
BD74-161	-99.3	491.4*	118.2	170.1*
BD74-222	8.1	199.2*	323.3	176.9*

* means significant effects

SCAs for yellow hybrid maize: The SCA for the grain yield of the yellow maize at Kisi, Ibadan, Iwo, and across the three locations are in Table 5. Thirty-two yellow hybrids had significant positive SCA effect in at least one location or across locations. A total of 21 hybrids had significant positive SCA at Kisi while 17, 11 and 15 hybrids had significant positive SCA at Ibadan, Iwo and across locations, respectively. Six hybrid combinations consisting of TZEI13 × BD74-161, TZEI16 × TZEI8, TZEI128 × TZEI16, TZEI11 × TZEI124, TZEI11 × BD74-222 and TZEI16 × BD74-165 had significant positive SCA in the three locations and across locations. The TZEI13 × TZEI128, TZEI12 × BD74-165, TZEI128 × BD74-165 and TZEI124 × BD74-222 had positive significant SCA in two locations and across locations. The SCA ranged from -975.9 to 1707.4 at Kisi, from -1328.0 to 1275.0 at Ibadan, and -657.4 to 1129.0 at Iwo, but -290.3 to 1345.0 across locations.

Contributions of female and male for grain yield of the white and yellow maize at three locations

Male and female parents contributed differently to the performance of the hybrid maize with respect to grain yield (Table 6). The effect of SCA was higher than that of GCA at the three locations and across locations for the white maize. However, the SCA effect was higher than GCA for yellow maize at Kisi and across locations only. The effects of GCA and

SCA for the yellow maize were similar at Iwo location but GCA was higher than SCA at Ibadan. The GCA_m was greater than GCA_f for the grain yield at all the locations and across locations for white maize. On the other hand, GCA_f was greater than GCA_m for the trait at all the locations and across locations for yellow maize.

Discussion

The significant mean square due to genotypes is an indication of genetic actions in the expression of the hybrids for grain yield, thus the possibility of effective selection. Significant $G \times E$ interaction shows that the hybrids responded differently to different environments. The significance may be attributed to the differences in environmental conditions. Babatope et al. (2020) has also found maize varieties respond different to change in growing conditions created by the environment. Similarly, significant female × male suggests the divergence of males from females for the two types of maize in all the locations. This finding is in agreement with Makinde et al. (2023) who confirmed a large variability in inbred lines of maize from different origins. However, the non-significant interactions of Environment × Female and Environment × Male shows that the parent materials reacted similarly either as male or female in different environment. Hence, the.

Table 4. Specific combining ability for grain yield of selected white maize hybrids evaluated at Kisi, Iwo, Ibadan, and across locations in 2014 and 2015

Hybrid	Kisi	Ibadan	Iwo	Across locations
TZEI1×TZEI4	-1101.8	133.5	2319.1*	450.3
TZEI1× TZEI98	1431.0*	-674.6	437.4	397.9
TZEI7× TZEI98	149.7	1445.7*	248.7	614.7
TZEI22× TZEI106	805.5	-426.7	1460.4*	613.1
TZEI136× TZEI98	-821.7	586.8	1467.4*	410.8
TZEI136× TZEI106	1102.5*	112.8	-730.2	161.7
TZEI188×TZEI2	1439.7*	-93.0	-787.2	186.5
TZEI188× TZEI4	42.8	1127.9*	660.8	610.5
BD74-152× TZEI7	-1143.1	57.7	1595.9*	170.1
BD74-147× TZEI136	1559.0*	131.6	-551.2	379.8
BD74-31×TZEI22	1582.0*	-95.2	607.8	698.2
BD74-55× TZEI22	1204.5*	-530.9	245.9	306.5
BD74-128× TZEI136	95.0	729.1*	-124.6	233.2
BD74-128×TZEI188	1201.5*	286.7	381.5	623.2
TZEI1×BD74-179	493.2	918.5*	122.3	511.3
TZEI1×BD74-399	-109.7	1096.9*	917.6	634.9
TZEI7×BD74-171	1474.9*	-452.9	-892.9	43.0
TZEI22× BD74-170	-1550.0	219.5	2763.8*	477.8
TZEI22×BD74-171	-900.5	-67.5	1033.9*	22.0
TZEI136×BD74-175	1432.2*	-243.2	-143.1	348.7
TZEI136× BD74-399	1312.6*	-223.4	-413.5	225.3
TZEI188× BD74-179	-741.9	254.5	1529.9*	347.5
TZEI2× BD74-31	270.0	966.7*	-597.9	212.9
TZEI2× BD74-55	1793.7*	-218.7	53.5	542.9
TZEI2× BD74-128	1302.8*	427.1	-157.0	524.3
TZEI4×BD74-152	2868.5*	559.1	-181.7	1081.9*
TZEI4×BD74-128	-120.5	-749.1	1211.0*	113.8
BD74-170×TZEI3	1906.5*	78.5	413.0	799.4
BD74-170× TZEI106	1221.7*	737.1*	-271.3	562.5
BD74-179×TZEI4	922.8	1347.7*	-662.3	536.1
BD74-399× TZEI106	-685.7	1011.6*	-107.9	72.7
BD74-170×BD74-31	146.0	-392.3	2772.8*	842.2
BD74-171×BD74-152	1934.6*	695.7	-1333.6	432.2
BD74-179×BD74-31	-382.0	717.1*	722.7	352.6
BD74-175×BD74-147	580.7	1028.9*	3179.8*	1596.5*
BD74-175× BD74-31	413.2	1103.2*	-1209.6	102.2
BD74-399× BD74-147	828.8	1130.1*	-803.5	385.1
BD74-399× BD74-55	-829.1	1209.8*	869.7	416.8
BD74-399×BD74-128	2261.2*	-181.9	124.1	734.5

Table 5. Specific combining ability of the yellow maize inbred lines in hybrids evaluated at Kisi, Iwo, Ibadan, and across locations in Nigeria in 2014 and 2015.

Hybrid	Kisi	Ibadan	Iwo	Across locations
TZEI13×TZEI146	-975.9	744.8*	-639.8	-290.3
TZEI13×TZEI128	1123.2*	987.2*	203.6	771.3*
TZEI13×TZEI8	782.5*	363.4	330.2	492.0*
TZEI13×TZEI124	747.0*	420.3	847.7*	671.6*
TZEI13×BD74165	41.5	352.3	1129.0*	507.6*
TZEI13×BD74161	1707.4*	983.2*	584.4*	617.9*
TZEI146×TZEI128	774.8*	103.3	-127.7	250.1
TZEI146×TZEI11	455.2	-487.6	494.5*	154.0
TZEI146×TZEI8	814.0*	145.1	-452.0	169.0
TZEI146×BD74165	-214.7	564.6*	-130.8	73.0
TZEI146×BD74222	-322.1	-1328.0	-47.7	-57.0
TZEI10×TZEI12	1421.4*	-44.3	173.1	516.7*
TZEI10×TZEI16	1498.3*	-116.1	200.8	527.7*
TZEI10×BD74-165	886.7*	-76.0	248.5	353.1
TZEI10×BD74222	-953.6	482.3*	-304.0	-258.4
TZEI12×TZEI128	650.5*	42.5	40.2	244.4
TZEI12×TZEI8	755.7*	542.7*	362.2*	431.9
TZEI12×BD74161	541.6	1250.0*	472.4*	754.7*
TZEI128×TZEI8	743.7*	-841.4	-20.4	-39.4
TZEI128×TZEI16	1152.8*	726.7*	485.6*	543.6*
TZEI128×BD74165	672.1*	145.8	-7.3	270.2
TZEI128×BD74161	-335.7	1275.0*	466.1*	468.4*
TZEI11×TZEI16	370.6	955.1*	190.5	505.4*
TZEI11×TZEI124	1955.0*	1243.0*	836.3*	1345.0*
TZEI11×BD74222	1270.7*	807.8*	696.6*	925.0*
TZEI8×TZEI124	-285.5	799.6*	63.8	192.6
TZEI8×BD74165	982.5*	-885.9	-657.4	-187.0
TZEI16×TZEI124	1159.0*	-76.6	-389.2	231.1
TZEI16×BD74165	751.3*	328.2*	543.8*	553.1*
TZEI16×BD74222	905.8*	447.3*	183.4	244.3
TZEI124×BD74222	1290.3*	689.9*	-54.2	642.0*
BD74165×BD74161	-886.5	511.5*	-152.8	-175.9

inbred lines can be used as male or female in the any of the environments

It has been earlier reported that lines derived from the same population may have either good or poor general combining ability (Lubadde et al., 2016). The significant effects of GCA indicates

that at least one of the maize lines differed in favourable genes with additive effects, while the significance of SCA indicates complementation between lines with some degree of non-additive effects. Additive and non-additive effects were highly significant and were responsible for

Table 6. Percentages of cross sums of squares contributed by GCA from female and male parents for grain yield of white and yellow maize evaluated at Kisi, Iwo, Ibadan and across locations in 2014 and 2015

Trait	Location	Percentage of cross sums of squares		
		GCA _f	GCA _m	SCA
White endosperm maize	Kisi	21	25	54
	Ibadan	18	22	60
	Iwo	17	24	59
	Across	21	27	52
Yellow endosperm maize	Kisi	21	9	70
	Ibadan	39	14	47
	Iwo	28	22	50
	Across	31	13	56

GCA_f: general combining ability of female; GCA_m: general combining ability of male; SCA: specific combining ability

the genetic expression of grain yield in the hybrid maize in the various locations. This agrees with the findings of Sibiyi et al. (2013) who found significant GCA and SCA for grain yield of maize in different environments. Additive, non-additive or both additive and non-additive gene actions were responsible for inheritance of grain yield of maize under various levels of soil N.

Ifie et al. (2015); Annor and Badu-Apraku (2016); Ige et al. (2017); Ertiro et al. (2020); Abu et al. (2020) reported additive gene actions-controlled inheritance of grain yield in maize, while Makumbi et al. (2011); Badu-Apraku et al. (2016); Annor et al. (2019); Makinde et al. (2023) reported that non-additive gene effects largely regulated grain yield under the N stress. Noëlle et al. (2017); Ogunniyan et al. (2019a), Badu-Apraku et al. (2021) also found that both additive and non-additive genes conditioned inheritance of grain yield under varied N conditions. The significant positive GCA of white endosperm lines BD74-128, BD74-171, BD74-55, BD74-31 and BD74-170 at Kisi suggests that the inbred lines possess favourable genes with additive effects. Incidentally, the five parent lines are exotic which can be exploited for higher grain yield improvement specific to the agro-ecology.

The BD74-171, BD74-179 and BD74-170 can also be used in developing high yielding white maize hybrids for cultivation in Ibadan. However, four local and exotic inbred lines

(TZEI7, BD74-179, BD74-175 and BD74-399) with significant positive GCA can be tracked for improvement of high yielding white maize hybrids adapted to Iwo and similar environments. The BD74-171, BD74-179 and BD74-170 are found suitable for hybrid development in at least one other location outside Ibadan. Inbred lines BD74-171 and BD74-170 are identified for Kisi, and BD74-179 for Iwo. The three lines may be utilized in the development of improved white maize stable across the locations because of their significant positive GCA across locations.

Moreover, inbred lines TZEI18 and TZEI16 which had significant positive GCA may be used in the development of high yielding yellow maize for cultivation at environments similar to Kisi condition. The BD74-165, BD74-161 and BD74-222 will make good parents for high yielding maize at Ibadan because of their high positive significant GCA. In Iwo location, yellow endosperm TZEI13 and TZEI12 had high positive GCA suggesting that they can be utilized in the breeding programmes aiming at developing high yielding yellow maize for farmers in the location. However, TZEI12, TZEI16 BD74-161 and BD74-222 had significant positive GCA across locations thereby offering themselves for utilization in consequent breeding programmes focusing on improvement for high grain yield with good stability across the agro-ecologies.

The higher effects of SCA over GCA (greater than 50% of the variation) in all the locations and across for white maize shows various levels of specific contributions of non-additive genes to expression of grain yield in the locations. Similarly, SCA was higher than GCA for grain yield of yellow maize in Kisi and across locations suggesting that non-additive genes action-controlled inheritance of the grain yield. Aminu et al. (2014); Pádua et al. (2016); Annor et al. (2019); Kamara et al. (2021) had also reported that inheritance of grain yield is controlled by non-additive gene effects. On the other hand, higher GCA effect observed in Ibadan and similar effects of GCA and SCA for the maize in Iwo show additive, and both additive and non-additive genes actions are responsible for inheritance of the trait in the respective locations. This agrees with findings of Premlathan and Kalamani (2010); Ige et al. (2017) that genetic expression of grain yield of maize is controlled by both additive and non-additive genes. However, the reports of El-Badawy (2013); Salami and Agbowuro (2016); Ige et al. (2020) that the additive gene effects played an effective role in the inheritance of grain yield supported the results for Ibadan location. These results prove that yield performance of the hybrids is location specific and should not be relied upon as a selection index without further analysis for the effects of $G \times E$. The male effects were greater than female effects which is an indication that male parents were genetically diverse than the female parents for white endosperm maize. Unlike the white maize, the female effects were more prominent than male effects on the grain yield of the yellow endosperm maize.

Despite that more than 10 hybrids had significant SCA for grain yield in at least one of the three locations, only white hybrids BD74-175×BD74-147 and TZEI4×BD74-152 had significant SCA across the locations. Hence, the white hybrid was identified as promising and can be recommended for further trials for use of farmers across the locations. Based on the significant positive SCA of hybrids BD74-170×TZEI106 and TZEI4×BD74-152 in more than one location, the hybrids can also be selected

as promising in the locations. Four most prominent hybrid combinations based on high significant positive SCA in Kisi were BD74-399 × BD74-128, BD74-171 × BD74-152, BD74-170 × TZEI3 and TZEI4 × BD74-152. Hybrids BD74-399 × BD74-55, BD74-179 × TZEI4, TZEI188 × TZEI4 and TZEI1 × TZEI4 were prominent in Ibadan. In Iwo, hybrids BD74-175 × BD74-147, BD74-170 × BD74-31, TZEI188 × BD74-179 and TZEI22 × BD74-170 were most promising combinations. The hybrids can be recommended for the respective locations.

Greater than 50% of hybrid combinations that had significant positive SCA in each of the locations were from crosses between IITA and CIMMYT lines. This could be proved by at least four hybrid combinations with significant SCA in each of the locations. One of the two hybrids with significant positive SCA across locations combined local and exotic inbred lines and the other was a combination of two exotic lines. The result confirms that introduction of exotic lines with novel genes can be explored for maize improvement. Crosses between species of crops from different background have been reported to be capable of producing improved novel types of the crops (Adebayo et al., 2014; Ogunniyan et al., 2019b; Mukul et al., 2020). This study shows that hybrids with significant SCA effects usually involve low, high and average general combiners. This further indicates that the involvement of at least one good combiner achieved some better specific cross combinations. Kisi location had the highest number of hybrids with significant SCA while Ibadan was the next with about 36 % and 26 % in Iwo. Combinations between parents with high GCA and low GCA resulting to high SCA effect have been reported to be attributable to favourable additive effects of the good general combiner and epistatic effects of the other parent (Milić et al., 2011; Dey et al., 2014).

A total of six hybrid combinations consisting of yellow hybrids TZEI13×BD74-161, TZEI16 × TZEI8, TZEI128 × TZEI16, TZEI11 × TZEI124, TZEI11 × BD74-222 and TZEI16×BD74-165 had significant positive SCA in the three locations and across locations. The hybrids may be nominated for further research for possible release for

farmers' use in the agro-ecologies. Variation in the ranges of SCA indicates that the response of each inbred line is different and specific to environment. The wider variations in Kisi and Ibadan than Iwo and across locations also buttress the variability in the performance of the yellow hybrids. However, the SCA effects were higher than GCA for yellow maize in Kisi and across locations only. Hence, the grain yield was controlled by non-additive genes actions. However, additive gene actions were responsible for the inheritance of the trait in Iwo while both additive and non-additive were responsible in Ibadan. Reports of El-Badawy (2013); El-Hosary and Elgammaal (2013) had shown that the non-additive gene actions represented the major role in the inheritance of grain yield of maize. Unlike in the white maize, effects of female were more preponderant than male in the three locations and across locations for the yellow maize. Hence, the role of the maternal parent was more important in the expression of the grain yield.

Conclusion

White inbred lines BD74-171, BD74-179 and BD74-170 as well as yellow inbred lines TZEI12, TZEI16 BD74-161 and BD74-222 are suitable for developing high grain yield maize with good stability under low N across agro-ecologies. White hybrid BD74-175 × BD74-147, BD74-170 × TZEI106 and TZEI4 × BD74-152 are most promising in more than one location. Yellow hybrids TZEI13 × BD74-161, TZEI16 × TZEI8, TZEI128 × TZEI16, TZEI11 × TZEI124, TZEI11 × BD74-222 and TZEI16 × BD74-165 are promising under low N across locations. Non-additive gene actions controlled the inheritance of the trait of both types of maize under low N in Kisi and across locations. Additive gene actions-controlled inheritance of the grain yield of the yellow maize under low N in Iwo while both additive and non-additive were responsible under the same condition in Ibadan. Hence, gene actions are location specific for yellow maize.

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