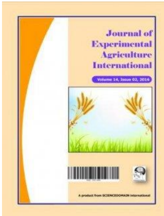

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Estimation of Combining Ability and Gene Actions in Maize for Grain Yield and Selected Agronomic Traits under Contrasting Soil Nitrogen Conditions

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Authors' contributions

This work was achieved by various efforts in collaboration of the authors. Author DJO conceived the idea, designed the study, performed the statistical analysis and interpretation of the data and wrote the first draft of the manuscript. All the authors participated in the field work, data collection and final manuscript writing and approval.

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ABSTRACT

Background: High cost, cropping pressure on soil and climate change are currently posing constraint to maize production in Africa. Development of, and genetic studies on adapted varieties of the crop might be useful to overcome the challenge.
Aim: To determine combining ability and gene actions of the maize inbred lines in their crosses under contrasting nitrogen conditions.
Materials and Methods: 150 hybrid maize generated from 20 inbred lines were evaluated in 2014 and 2015 in low and optimal N conditions in an experiment laid out in 19 × 8 lattice design with three replicates. Days to anthesis (DTA) and days to silking (DTS) were counted. Anthesis-silking-interval (ASI) and grain yield (GY) were estimated. Plant and ear heights were measured while stay green (SG), plant aspect (PASP) and ear aspect (EASP) were scored. Analysis of variance was performed on the data collected. The general combining ability (GCA), specific combining ability (SCA) and

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relative contribution of GCA and SCA on progeny for agronomic performance were also estimated.
Results: Significant differences existed due to environments, genotypes, male, female and female × male for GY and other traits. Only BD74-171, BD74-179, BD74-170 and BD74-175 had significant high GCA effects for GY under low N. The BD74-128, BD74-171, TZEI188, BD74-55, TZEI1, BD74-179, BD74-175 and BD74-399 had significant GCA effects under optimal N. Only 23 of the 150 hybrids had significant high SCA in at least one of the N conditions. From these, 14 and 15 hybrids had high positive and significant SCA in low and optimal N conditions, respectively. The GCA and SCA varied for all the traits signifying prominence of both additive and non-additive genetic components.
Conclusion: Inheritance of GY, DTA, DTS and SG are governed by non-additive gene action but vice versa for PH and EH under both N conditions. Effects of male were greater than those of female in gene expression for the GY under the N conditions, but males were genetically diverse than females for the other traits in the low N condition. Effects of both male and female are important in inheritance of flowering and growth parameters under optimal N condition.

Keywords: Combining ability; gene action; hybrid; parental effects; nitrogen tolerance.

1. INTRODUCTION

Maize (*Zea mays* L.) is one the most important and widely grown cereal in the world. It is important for food, feed and as raw materials for numerous industries. Currently, there is a wide gap in the supply and demand for the crop all over the world. Productivity of the crop varies with the change in the effects of climatic and edaphic status. Mean grain yield (GY) in Nigeria ranges between 1.0 and 2.0 t ha^{-1} while mean world's maize GY was 5.5 t ha^{-1} in 2013. Up to 8.6 t ha^{-1} was realisable in the temperate countries [1]. A major limitation to high productivity of the crop in Africa is low level of soil nitrogen (N) [2,3]. This has made application of nitrogen fertiliser powerful to replenish the soils that are deficient in the nutrient inevitable in maize producing area [4]. The nutrient is necessary to promotes growth and fruiting with respect to kernel initiation, setting and filling. Continuous cultivation of soil for crops for the ever increasing human and livestock populations coupled with the current climatic change had resulted in depletion of the soil nutrients. This had drastically reduced maize yield over the years on the farmers' fields, despite the enormous scientific intervention to improve the crop's agronomic performance. Annual loss of up to 50% in the grain yield of maize due to N insufficiency has been reported [5].

However, overuse of fertiliser results in higher environmental risks and waste of energy applied to the industrial synthesis of the fertilisers [6]. Besides, fertiliser as a mean of nutrient management is expensive thereby adding to total cost of production. This has made most African farmers who mainly depend on the natural soil fertility reject the use of fertilisers for crop production. Fertilisers are reportedly applied at the rate of 10 kg ha^{-1} in Africa compared to the global rate of 100 kg ha^{-1} and 200 kg ha^{-1} in Asia [7]. In Africa where fertiliser use is minimal, genetic approaches are therefore essential to attain sustainable production of high yield of maize at reduced rates of N despite the poor soil fertility status. The improvement should begin with selection among the germplasm already identified for such programmes. Selection of parental genotypes based on combining ability has been used as an important approach in crop improvement [8]. Combining ability has become increasingly important to plant breeders because of the widespread use of the hybrids in many crops. Appropriate decisions in the development of hybrid maize are made with the application of the concept.

Combining ability explains the combination among inbred lines during hybridisation process where desirable genes are transferred to subsequent generations. The concepts of GCA and SCA cannot be overemphasised in plant breeding because it helps to estimate the genetic values, characterise the nature and magnitude of genetic effects governing yield and other agronomic traits as well as suitability of inbred lines for hybridisation [9,10]. Analysis of the combining ability of inbred lines identifies the promising combiners and determine their potential value for hybridisation to exploit heterosis and to select better crosses for direct use or further breeding programme [11]. Significant GCA effects may also be used to estimate gene action of traits while the SCA is used to identify the best cross combinations for hybrid production [12]. The knowledge of genetic actions and mode of inheritance of different traits help breeders to effectively employ suitable breeding methodology for their improvement [13]. Soils of the tropics are fragile and friable hence the nutrient elements, especially N are lost rapidly. All efforts to replenish soil nutrients have not produced desired results. A cheap and effective option is to use of breeding approach. Therefore, the primary aim of this study was estimate combining ability and determine the gene actions effects for grain yield and selected agronomic traits in crosses of the inbred lines under varied N conditions.

2. MATERIALS AND METHODS

2.1 Germplasm and Experimental Site

One hundred and fifty single cross hybrid maize were generated from 20 inbred lines using North Carolina Design II mating design in 2013. The hybrids were evaluated in 2014 and 2015 under the varied soil N conditions. The test hybrids were evaluated with two check hybrids. The trial was conducted in soil depleted of its native N before commencement of the trial in Ibadan, Nigeria (3.56° E; 7.33° N and 168 m above sea level). Maize were planted a very high population density without application of fertiliser. All the maize plants were uprooted and removed from the field shortly before flowering. Soil analyses were done to ascertain N had been totally removed before the trial. Mean annual rainfall and temperature of the experimental site were 186.9 mm and 26.1°C, respectively.

2.2 Experimental Layout and Crop Management

The experiment was laid out in 19 × 8 lattice design with three replicates. Plots consisted of two rows of 5 m long and 0.75 m apart, where plants were spaced 0.5 m in a row. Three seeds were sown and later thinned at 2 WAP to two stands per hill to attain a plant population of 53,333 plants ha^{-1}. There were two N concentrations, namely 30 and 90 kg N ha^{-1} denoting low and optimal N conditions, respectively. The fertiliser was applied in the form of NPK 15:15:15 at 30 kg ha^{-1} to each of N conditions plots at 4 WAP. The optimal N condition plots also received 60 kg N ha^{-1} in the form of urea to bring the total available N to 90 kg ha^{-1} two weeks later. All the plots received 60 kg P ha^{-1} as SSP and 60 kg K ha^{-1} as muriate of potash. Standard cultural practices were applied for field maintenance, harvesting and seed processing according to the recommendations of IAR&T 2010 [14].

2.3 Data Collection and Analysis

Days to anthesis (DTA) and days to silking (DTS) were counted as the number of days from planting to 50% pollen shed and 50% silking emergence, respectively. Anthesis-silking-interval (ASI) was estimated as the differences between DTS minus DTA. Plant and ear heights were heights of the plant from soil surface to the base of tassel and base of uppermost ear, respectively. Stay green (SG) was scored [15], three times at eight days apart during the latter part of grain filling on a scale from 0 to 10, by dividing the percentage of estimated total leaf area that were dead by 10. Scale 1 = 10% of leaves are dead, 2 = 20 %, 3 = 30 %, 4 = 40 %, 5 = 50 %, 6 = 60 %, 7 = 70 %, 8 = 80%, 9 = 90 % and 10 = 100 % of the leaves were dead. Plant aspect (PASP) was visual assessment of quality scored on plot basis before harvest, after flowering (at brown silk stage) when plants were still green and ears fully developed on scale 1 to 5 where 1 = excellent; 5 = very poor. General appeal of the whole row plants, based on the relative plant and ear heights, uniformity of the plant stand, reaction of plants to diseases and insects as well as lodging was considered in the plant aspect scoring. Ear aspect (EASP) was also visual assessment of quality scored on a scale of 1 to 5 where 1=excellent; 5=very poor. The score was taken on the pile of harvested ears of each plot when spread out and the general look of the ears is taken into account. Ear size, uniformity of colour and texture, grain fill, disease and insect damage were considered for this score.

The ears of the plants were harvested when dry. The grains were shelled and weighed after which the moisture content was determined using a digital moisture tester. Grain yield in kg ha^{-1} was computed using grain moisture content = 15%, harvested plot area = 7.5 m^2 and 1 ha = 10,000 m^2 as follows:

$$\text{Grain yield (kg ha}^{-1}) = \frac{\text{GWT (kg)}}{7.5\text{ m}^2} \times \frac{(100-\text{MC})}{(100-15\%)} \times 10{,}000\text{ m}^2$$

where GWT = grain weight and MC = grain moisture content at harvest.

Analysis of variance was performed on the data collected for the 150 test and two check hybrids according to NCD II, with hybrids nested within sets for each environment (1 N concentration × 2 years) using SAS [16]. Main effects due to male and female were independent estimates of GCA while effects due to male × female were the SCA for grain yield and other traits considered, for each N condition. The GCA effects of female and male parents were tested for significance using their interaction as the error variance. The SCA effects were tested for significance using the error variance pooled across sets. The general linear model for the NCD II mating design [17] is:

$$X_{ijkl} = \mu + m_i + f_i + (mf)_{ij} + p_{ijk} + r_i + \varepsilon_{ijkl}$$

where X_{ijkl} = the observed value of the progeny of the i^{th} male crossed with j^{th} female in the k^{th} replicate; μ = the overall population mean; m_i = effect of the i^{th} female; f_j = the effect of the j^{th} male mated to the i^{th} female; $(mf)_{ij}$ = the interaction effect between the i^{th} female and the j^{th} male; p_{ijk} = the effect of the k^{th} progeny from the cross between i^{th} female and j^{th} male; r_l = the effect of the r^{th} replicate; ε_{ijkl} = the experimental error.

The cross sums of squares were partitioned to determine the relative contributions of male and female GCA effects. The mean square ratio for GCA and SCA is used to reveal the nature of gene action involved in expression of quantitative traits. The closer the ratio is to 1, the higher the probability that progeny performance can be adequately predicted from GCA, and the closer this ratio is to zero, the greater the importance of SCA in predicting progeny performance. High strength of GCA effects for a particular trait implies that additive genetic effects are more important for the inheritance of that trait, while non-additive genetic effects were more important for a trait for which SCA effects are predominant.

3. RESULTS

3.1 Grain Yield and Other Agronomic Traits of the Hybrid Maize in Varied N Conditions

Mean squares of the ANOVA for GY and other agronomic traits of the 152 hybrid maize evaluated in low and optimal N conditions across 2014 and 2015 are presented in Table 1. Significant differences existed due to environments, sets, genotypes, male, female and female × male for GY and other traits. The effect of G × E was significant for all the traits except ASI, PASP and EASP. Effects of the environment × female (E × F) and environment × male (E × M) were not significant for the traits in the low N condition. In optimal N condition, the effects of environments, set, genotypes, male, female and female × male for the GY and other agronomic traits of the maize were significant. The G × E also had significant effect for all the traits except ASI and PASP, while the effects due to E × F and E × M were not significant except E × F for DTA and DTS and effect of E × M was significant for DTS and ASI (p<0.5).

Mean grain yields of the hybrid maize under low and optimal N were 3631.53 kg ha^{-1} and 4840.93 kg ha^{-1}, respectively (Table 2). The GY ranged from 1494.95 to 6238.73 kg ha^{-1} under low N condition while the range was from 2320.58 to 7940.91 kg ha^{-1} for optimal N condition. The mean DTA under the two N conditions were similar but DTS and ASI were lower under optimal N condition. Similarly, the PH was similar under the two N conditions (about 113 cm) while EH was higher under optimal N (45 cm) than low N condition (44 cm). It was found that scores of SG, PASP and EASP were over 3.0 under low N while the scores were less than 3.0 under optimal N condition. The CVs were lower for GY, DTA, DTS and ASI under optimal N while the parameter was similar for other traits under both N conditions.

3.2 Estimation of Combining Abilities for Grain Yield of the Maize Inbred Lines

GCAs for the grain yield of the maize inbred lines in varied N conditions. Estimates of GCA effects of female (GCA_f) and male (GCA_m) for GY of the 20 inbred lines evaluated in hybrids of the inbred lines in sets over the two years in low and optimal N conditions are shown in Table 3. Only three inbred lines namely BD74-171, BD74-179 and BD74-170 had positive and significant GCA_f effects for GY while BD74-170 and BD74-175 had positive and significant GCA_m effects in low N condition. However, BD74-128, BD74-171, TZEI188, BD74-55 and BD74-399 had positive and significant GCA_f effects for the trait, and the GCA_m of TZEI1, BD74-179 and BD74-175 were positively and significant in optimal N.

SCAs for grain yield of the white maize inbred lines in varied N conditions. The SCAs and SCA ranks for GY of selected hybrids under the contrasting N conditions are presented in Table 4. The selected hybrids were 23 of the 150

Table 1. Mean squares of yield and other agronomic traits from the analysis of variance for hybrid maize evaluated under varied N conditions in 2014 and 2015

Source of variation	Df	Grain yield	DTA	DTS	ASI	Plant height	Ear height	Stay green	PASP	EASP
Low N (30 kg ha^{-1})										
Environment (Env.)	1	167603.7*	148.00***	161.12***	0.28*	3269.77***	142.87*	0.80*	4.59***	1.22*
Set	5	23436136.2***	35.58***	30.63***	3.63***	489.89***	96.48*	6.91***	1.31***	1.01***
Env × set	5	729107**	3.24***	4.05**	0.23**	62.27^{ns}	52.15^{ns}	0.07^{ns}	0.41*	0.37^{ns}
Replicate (Env.)	4	937539.7*	2.60**	2.81**	0.40*	3397.78***	300.46***	1.01***	1.50***	1.63***
Block (Env. × replicate)	108	284683.6^{ns}	1.45***--	1.69***	0.32*	420.10***	110.48***	0.43***	0.30***	0.25*
Genotype	151	2824967***	5.83***	6.75***	1.42***	677.32***	280.10***	1.18***	0.45***	0.61***
Genotype × Env	151	1063090.6***	1.64***	1.96***	0.22^{ns}	200.09*	63.13***	0.39***	0.18^{ns}	0.23^{ns}
Female (set)	24	2218593.0**	7.24***	8.64**	2.25***	1327.22***	631.65***	1.52***	0.47**	0.95***
Male (set)	24	2689277.0*	4.53*	5.02*	1.06***	1039.03***	376.34***	1.19***	0.35*	0.90**
Female × Male (set)	96	1851168.0**	3.93***	5.25***	1.16***	390.52**	163.56***	0.72**	0.41***	0.38**
Env. × Female (set)	24	811863.0^{ns}	2.59 ^{ns}	2.53 ^{ns}	0.20^{ns}	150.78^{ns}	111.52**	0.36^{ns}	0.17^{ns}	0.18^{ns}
Env. × Male (set)	24	1270791.0^{ns}	1.77^{ns}	2.16^{ns}	0.21^{ns}	109.45^{ns}	33.27^{ns}	0.31^{ns}	0.17^{ns}	0.19^{ns}
Env. × Female × Male(set)	96	1077405.0^{ns}	1.24***	1.63**	0.23^{ns}	216.61*	54.45	0.41***	0.14^{ns}	0.21^{ns}
Pooled error	488	283184.3	0.72	0.97	0.34	153.41	42.103	0.21	0.16	0.19
Optimal N (90 kg ha^{-1})										
Environment (Env.)	1	20264298.8***	292.10***	375.94***	5.28***	6131.90***	7959.70***	2.56***	0.07^{ns}	0.35^{ns}
Set	5	21849355***	50.68***	46.06***	0.62*	313.52^{ns}	72.03^{ns}	6.70***	1.25^{ns}	3.68***
Env × set	5	2683578**	6.87***	7.12***	0.60*	322.55*	39.42*	0.94***	0.17***	0.19^{ns}
Replicate (Env.)	4	2212723.2*	1.92^{ns}	2.80*	0.31^{ns}	1138.02***	241.34**	1.27***	1.55^{ns}	0.67**
Block (Env. × replicate)	108	1006728.4***	1.77***	2.01***	0.30^{ns}	451.92***	166.09***	0.26**	0.25*	0.32***
Genotype	151	4991746.6***	12.11***	13.21***	1.12***	821.26***	343.57***	1.17***	1.02***	1.03***
Genotype × Env	151	2045634.1***	3.11***	3.45***	0.22^{ns}	287.78***	112.04***	0.49***	0.19^{ns}	0.23***
Female (set)	24	5012581.0**	9.06*	267.66*	1.44***	1365.87**	539.09**	1.34**	0.79**	1.28**
Male (set)	24	6410435.0**	21.70***	521.99***	0.74**	1263.37***	609.58***	1.17*	0.79***	1.10***
Female × Male (set)	96	3529115.0**	7.61***	8.92***	1.12***	595.99***	229.90***	0.72**	1.00***	0.80***
Env. × Female (set)	24	1837256.0^{ns}	4.48*	5.01*	0.23^{ns}	400.89^{ns}	164.94^{ns}	0.38^{ns}	0.27^{ns}	0.39^{ns}
Env. × Male (set)	24	1925789.0^{ns}	3.44^{ns}	4.35*	0.33*	209.89^{ns}	67.17^{ns}	0.53 ^{ns}	0.19^{ns}	0.24 ^{ns}
Env. × Female × Male(set)	96	2073133.0***	2.32***	2.43***	0.18^{ns}	276.51***	113.63***	0.47***	0.19^{ns}	0.20 ^{ns}
Pooled error	488	656333.0	0.87	1.03	0.26	153.21	56.96	0.19	0.18	0.16

^{ns}, *, **, *** and df are not significant, significant at $p<0.05$, 0.01, 0.001 and degree of freedom, respectively. DTA, DTS, ASI, PASP and EASP are days to anthesis, days to silking, anthesis silking interval, plant aspect and ear aspect, respectively.

Table 2. Table of means for grain yield and other agronomic traits of 152 hybrid maize evaluated under low and optimal N conditions in 2014 and 2015

Trait	Low N				Optimal N			
	Mean	CV	Min	Max	Mean	CV	Min	Max
GY (kg ha^{-1})	3631.53	26.14	1494.95	6238.73	4840.93	23.36	2320.58	7940.91
DTA (days)	57.97	2.33	54.28	60.07	57.56	1.99	50.98	60.15
DTS (days)	60.21	2.47	55.61	62.42	59.39	2.09	51.85	61.99
ASI (days)	2.24	24.93	0.79	3.78	1.84	23.03	0.79	2.99
PH (cm)	113.15	11.99	77.94	145.98	113.03	11.42	85.57	156.03
EH (cm)	44.14	14.92	25.46	68.41	45.40	14.26	27.96	69.82
SG (1-10)	3.40	14.04	2.20	4.59	2.82	13.65	1.72	3.84
PASP (1-5)	3.03	14.80	2.14	3.80	2.75	14.19	1.32	4.10
EASP (1-5)	3.04	14.40	2.33	3.90	2.81	14.28	1.47	3.87

GY, DTA, DTS, ASI, PH, EH, SG, PASP and EASP are grain yield, days to anthesis, days to silking, anthesis silking interval, plant height, ear height, stay green, plant aspect and ear aspect, respectively.
CV, Min and Max are coefficient of variation, minimum and maximum, respectively.

Table 3. Estimates of female and male GCA effects for grain yield of 20 inbred lines evaluated in single cross hybrid maize under low and optimal N conditions in 2014 and 2015

Inbred line	Low N		Optimal N	
	GCA_{female}	GCA_{male}	GCA_{female}	GCA_{male}
TZEI106	-219.15	-165.26	-361.13	-85.68
TZEI2	-186.00	56.04	-536.70	101.05
BD74-128	170.13	150.51	623.44*	128.07
TZEI136	-644.46	-177.79	-714.42	-310.21
TZEI1	-457.76	78.82	-418.20	456.28*
BD74-152	241.28	-474.03	-248.26	-268.14
BD74-171	521.88*	194.05	804.37*	-160.75
TZEI98	-25.80	-367.2	-60.24	305.31
TZEI188	161.68	-158.88	491.05*	-407.18
TZEI4	-75.58	-447.82	-195.15	-669.20
BD74-55	173.58	-161.32	662.05*	-85.59
BD74-147	60.03	-101.48	221.83	-125.08
TZEI7	-19.37	-304.08	-326.66	61.69
BD74-31	225.17	-542.45	211.10	-727.51
BD74-179	412.32*	289.91	371.55	582.51*
TZEI3	-343.80	-513.71	-351.37	-245.20
TZEI22	-168.86	-309.93	-110.04	-553.24
BD74-170	497.03*	1034.43*	236.75	278.30
BD74-175	-644.29	584.37*	-964.58	676.63*
BD74-399	302.13	52.47	699.02*	211.98

** is significant effect. GCA_{female} and GCA_{male} represent general combining ability for female and general combining ability for male, respectively.*

developed hybrids which had significant SCA in both or at least one of the N conditions. From these, 14 and 15 hybrids had positive and significant SCA in low and optimal N conditions, respectively. Hybrids BD74-128×TZEI136, BD74-170×TZEI106, BD74-399×TZE106, BD74-175×BD74-147, BD74-399×BD74-147 and BD74-399×BD74-55 had positive and significant SCA in both N and condition N. Among the six hybrids that had positive and significant SCA in the two N conditions, BD74-170 × TZEI106, BD74-399 × TZE106 and BD74-175 × BD74-147 ranked among the first 10 in each of the N conditions.

3.3 Contributions of Female and Male GCA for Grain Yield of Maize in Two N Conditions

Partitioning the cross sums of squares of GCA effects for GY and other traits of the hybrid maize evaluated in two N conditions (Table 5) shows that GCA effects accounted for greater than 50% of the variation among the hybrids for PH and EH in both low N and optimal N conditions and EASP only in low N. The GCA effects captured between 40 and 49 % of the variations for GY, DTA, DTS and SG in low N and optimal N while it accounted for less than 40% of the variation in

Table 4. Specific combining ability and rank[1] for grain yield of selected maize inbred lines under low and optimal N in 2014 and 2015

Hybrid	Low N		Optimal N	
	SCA	SCA rank[1]	SCA	SCA rank[1]
TZEI7×TZEI98	1445.65*	1	-213.42	97
TZEI188×TZEI4	1127.89*	5	-148.56	93
BD74-152×TZEI7	57.66	68	1261.88*	9
BD74-31×TZEI136	570.21	22	1505.06*	6
BD74-128×TZEI136	729.06*	13	1778.62*	4
TZEI1×BD74-179	918.49*	11	-183.06	95
TZEI1×BD74-175	-280.87	105	999.86*	15
TZEI1×BD74-399	1096.87*	7	395.00	38
TZEI136×BD74-170	669.81	16	1256.25*	10
TZEI2×BD74-152	-673.67	138	1193.35*	12
TZEI2×BD74-31	966.73*	10	-566.97	119
TZEI4×BD74-31	206.65	53	1404.58*	7
TZEI106×BD74-128	547.52	25	1533.65*	5
BD74-170×TZEI106	737.07*	12	1346.22*	8
BD74-179×TZEI4	1347.73*	2	245.86	48
BD74-179×TZEI98	-288.76	106	1069.07*	13
BD74-399×TZEI106	1011.61*	9	1892.97*	3
BD74-171×BD74-147	401.44	35	1216.58*	11
BD74-179×BD74-31	717.06*	14	-210.11	96
BD74-175×BD74-147	1028.86*	8	2403.32*	1
BD74-175×BD74-31	1103.16*	6	651.02	25
BD74-399×BD74-147	1130.14*	4	1923.78*	2
BD74-399×BD74-55	1209.83*	3	1011.88*	14

SCA is specific combining ability

[1] means rank in the 150 hybrids generated and evaluated

Table 5. Percentages of hybrids sums of squares contributed by GCA and SCA effects for selected agronomic traits of maize evaluated under low and optimal N conditions in 2014 and 2015

Trait	N concentration	GCA_f	GCA_m	SCA
		Percentages of cross sums of squares		
Grain yield	Low	18	22	60
	Optimum	20	25	55
Days to anthesis	Low	26	16	57
	Optimum	15	35	50
Days to silking	Low	25	14	61
	Optimum	16	32	52
Anthesis silking interval	Low	28	13	58
	Optimum	22	11	67
Plant height	Low	34	26	40
	Optimum	27	25	48
Ear height	Low	38	23	39
	Optimum	26	29	44
Stay green	Low	27	21	51
	Optimum	25	22	54
Plant aspect	Low	19	14	67
	Optimum	14	14	72
Ear aspect	Low	28	27	45
	Optimum	23	20	57

GCA_f, GCA_m and SCA are general combining ability for female and general combining ability for male and specific combining ability, respectively.

PASP in the two N conditions. Differences attributable to SCA were greater than 50% for most traits in both N conditions. In low N condition, sum of squares for GCA_f was greater than GCA_m for all the traits except for GY. Sum of squares for GCA_m was greater than GCA_f for GY, DTA, DTS and EH and vice versa for ASI, PH, SG and EASP but similar for PASP in optimal N.

4. DISCUSSION

In this study, the GCA × environment effects were significant for DTA, DTS and ASI under optimal N. Hence, selection of promising lines based on the flowering traits in each environment (year) is necessary. Medici et al. [18] had earlier explained that the GCA × environment means inconsistency among additive effects of lines at contrasting N levels. The significant effects of GCA indicates that some maize lines differ in favourable genes with additive effects. Similarly, significance of SCA indicates some degree of non-additive effects. Additive and non-additive effects were highly significant and were responsible for the genetic expression of traits in the hybrid maize in low and optimal N conditions. It has also been earlier reported that lines derived from the same population may have either good or poor general combining ability [19].

The GY obtained in this study was averagely high compared with the mean value for Africa (1.0 and 2.0 t ha^{-1}) according to FAOSTAT, 2015 [1]. The lower values for DTS and ASI under optimal than low N condition explains the importance of N in the production of maize. This can also be responsible for the lower CVs for some of the traits under optimal N, thereby indicating more variability in the performance of the maize under low N than optimal N condition. Selection of promising varieties under stress N condition is therefore possible. Bänziger et al. 2000 [15]; [20] had in their studies found that grain yield, flowering traits and stay green-ability are suitable indicators in determining low N tolerance in maize.

The GCAs of the inbred lines for GY of the hybrid maize varied from low to high and from not significant to significant suggesting differential contributions of the lines in the crosses they were involved in different N conditions. The contribution of the inbred lines is specific with respect to the paternal or maternal effects. For instance, inbred lines BD74-171 and BD74-179 had high, positive and significant GCA effects for GY in low N when applied as female while BD74-175 contributed significantly as a male parent. However, only BD74-170 is suitable as male or female in crosses of the maize under low N condition. Similarly, GCAs of BD74-128, BD74-171, TZEI188, BD74-55 and BD74-399 are best as female and TZEI1, BD74-179 and BD74-175 were suitable as male in optimal N due to the positive and significant GCAs. Generally, BD74-171 and BD74-175 were promising female and male inbred lines, respectively notwithstanding the N condition. The effects of GCA can be used to select superior maize genotypes in low N condition and that high GCA effects indicate the presence of the desired alleles [21]. A high GCA estimate indicates higher heritability and less environmental effects and may lead to less gene interactions, thus higher achievement in selection [22].

The significant GCA effects for GY and other traits of the hybrid maize imply that additive gene action controls inheritance of the traits in respective N condition. The SCA for GY, DTA, DTS and SG were higher than those of GCA indicating non-additive effect in the control of the traits but it was vice versa for PH and EH in both N conditions. The GCA_m higher than GCA_f for GY suggests that the effects of male were greater than the female effects in gene expression for the trait in both N conditions. However, effects of GCA_f was greater than GCA_m for all other traits in low N only. This suggests that males were genetically diverse than females for the other traits in the low N condition. The GCA_m was greater than GCA_f for GY, DTA, DTS and EH and vice versa for ASI, PH, SG and EASP. The effects of GCA_f and GCA_m were similar for PASP indicating similar contributions of both female and male in gene expression for the trait in the N condition. Thus, effects of both male and female are important in inheritance of flowering and growth parameters under optimal N condition. This finding had shown the differences in the parental effects in inheritance of agronomic traits in maize grown under varied N conditions. Derera et al. [23] observed that higher female GCA effects compared to male GCA effects for GY and ASI may imply that maternal effects influence the expression of these traits.

The SCA effects were high in many of the hybrids especially for the GY indicating good specific combination and effects of non-additive genes for the trait among crosses. Conflicting reports have been obtained among authors on the gene action responsible for inheritance of maize GY. Several authors including Ojo et al. 2007 [24]; [12,19] reported that additive genetic action was more preponderance for inheritance of maize traits. On the contrary, [25,26,27] reported that grain yield, flowering and other traits are controlled by non-additive gene action. Betran et al. [28] had emphasised the importance of non-additive gene action in maize in low N conditions. Sibiya et al. [29] found highly significant GCA and SCA for GY in maize inbred lines evaluated in six environments but reported predominance of GCA over SCA effects in the inbred lines. Murtadha et al. [30] in their analysis of combining ability over environments in crosses of maize found that variability in the maize was attributable to additive and non-additive gene effects. Derera et al. [23] observed both additive and non-additive effects were important for ASI, DTA and DTS of maize under stress condition. The results in this study agreed with [18], who in their analysis of maize lines with contrasting responses to N found additive gene actions control inheritance of the GY under low N condition.

5. CONCLUSION

Inbred lines BD74-171, BD74-179 and BD74-170 had significant GCA_f effects for GY but BD74-170 and BD74-175 had significant GCA_m effects in low N condition. However, BD74-128, BD74-171, TZEI188, BD74-55 and BD74-399 had significant GCA_f effects while the GCA_m of TZEI1, BD74-179 and BD74-175 were significant in optimal N. Therefore, the lines could be utilised as sources of inbred lines for development of high yielding varieties for cultivation in respective N conditions. Non-additive gene effect controls inheritance of grain yield, days to anthesis and silking, and stay green of the maize while additive gene action governs inheritance of plant and ear heights under both N conditions. The effects of male were greater than those of female in gene expression for the grain yield in both N conditions. Males were genetically diverse than females for the other traits in the low N condition. Effects of both male and female are important in inheritance of flowering and growth parameters under optimal N condition. Hence, critical decisions have to be made in selection of parental lines.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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