Combining Ability and Heterosis of Tolerance to Low Soil Nitrogen in Tropical Maize Cultivars Derived from Two Breeding Eras

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Research Article

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Combining ability and heterosis of tolerance to low soil nitrogen in tropical maize cultivars derived from two breeding eras

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Abstract: Low soil nitrogen is one of the principal abiotic stresses affecting maize productivity in Sub-saharan Africa. Field studies were conducted at the International Institute of Tropical Agriculture (IITA), Ibadan during the cropping seasons for three years, from 2010 to 2012, with ten open pollinated maize varieties (OPVs) derived from two breeding eras (1 and 2). The ten OPVs and their crosses were evaluated under high-N and low-N conditions. The aim was to identify superior populations that may be useful sources genes for inbred line extraction and hybrid development for grain yield. Under low-N condition, mid and high parent heterosis for grain yield were low indicating the suitability of the hybrids for cultivation only in environments with high productivity index. Hybrid DMR-LSR-W (Era 1) × TZSR-Y-I (Era 2) had greatest mid and high-parent heterosis for grain yield under high-N and across the other four test environments. Parent AMATZBR-WC2B with higher general combining ability effects and mean values for grain yield, and cross combinations DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) and BR9922DMRSR (Era 2) x TZBRELD-4C0W (Era 2) with higher specific combining ability for grain yield under low-N environment are promising candidates for the development of nitrogen use efficient varieties for cultivation in low-N environments.

Keywords: Low nitrogen, *Zea mays* L. hybrid vigour, specific combining ability

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1 Introduction

The farmers' fields in the West and Central Africa is afflicted with low soil nitrogen (N) (Bello et al. 2014). During the period of sufficient rainfall, leaching of soil nitrogen beneath the plant root zones, which resulted to nitrogen stress (Bello et al. 2011). Poor weed control, crop residues removal for fuel and animal feeds worsened the soil nitrogen deficiency (Noëlle et al. 2017). Furthermore, many farmers applied nitrogen fertilizer at sub-optimum regimes due to the exorbitant prices of the inorganic fertilizer (Bello et al. 2011). Zea mays (maize) grain yield annual loss estimate range between 10 and 50% due to low N factor alone (Noëlle et al. 2017).

Development of better performance of crosses within the first generation (F_1) regarding their parents not only transformed maize breeding stratagem, but also created the basis of maize seed industry (Acquaah 2007). The effect of this paradigm shift resulted in the global maize yield production estimates (Kiani et al. 2015). The hybrid vigor contributed greatly to genetics of the agricultural world and meaningful expression in maize compared with other cereals. Furthermore, hybrid vigor is being exploited exhaustively by seed production companies and maize breeders (Kiani et al. 2015). An important aspect of hybrid maize breeding programme is the extraction of an elite group of inbred lines or identification of specific set of lines that maximize expression of heterosis in hybrid combinations. The concept of heterosis in maize improvement began with the studies reported by Shull (1908). Heterosis is described as the superiority of a hybrid or F_1 over the mean of its parents, which is referred to as the mid-parent (MP) heterosis or superiority of the F_1 or hybrid over the better parent, which is referred to as high-parent (HP) or better parent (BP) heterosis. In practical plant breeding, the superiority of F_1 over the mid-parent is not utilizable, because it does not offer the hybrid any advantage over the better parent. The development of hybrid combinations with high heterosis can be achieved through identification of good progenitors, or parents with desirable agronomic traits, and high general and specific combining ability. This has necessitated the grouping of various germplasms into distinct heterotic groups. Various heterotic pairs have been identified in various parts of the world for the development of hybrid combinations with high heterosis.

In quantitative genetic terminology, heterosis is interpreted as the superiority of a hybrid or F_1 over the mean of its parents, which is referred to as the mid-parent (MP) heterosis while the superiority of the F_1 or hybrid over the better parent, is referred to as high-parent (HP) heterosis (Nadarajan and Gunasekaran 2008). In practical plant breeding, the superiority of F_1 over the MP is not utilizable, because it does not offer the hybrid any advantage over the better parent. The development of hybrid combinations with high heterosis can be achieved through identification of good progenitors, or parents with desirable agronomic traits, and high general and specific combining ability Bajaj et al. (2007), and Jain and Bharadwaj (2014). This has necessitated the grouping of various germplasms into distinct heterotic groups. Various heterotic pairs have been identified in various parts of the world for the development of hybrid combinations with high heterosis. In an experiment conducted by Han et al. (1991) to examine the combining ability effects of inbred lines derived from maize population at International Maize and Wheat Improvement Center (CIMMYT) The authors' reported that inter-population crosses were superior by between 4 and 16 percentage (%) over the intra-population crosses for grain yield.

Estimation of combining abilities is one of the principal methods in identifying the best cross combinations that may be used either to exploit heterosis or accumulate desired alleles for the targeted traits. As a tool, it also facilitates the understanding of the genetic basis of expression of many characteristics that enable the plant breeder design effective breeding method for future improvement programmes. Many workers had reported that the parents that had high significant positive GCA effect showed the parents' *per se* performance. This also revealed the imperative and outstanding of additive effects as well as genetic diversity occurrence in the traits of studied. The workers further posited that this would allow selection in the hybrid combinations that had the best GCA with better performance (Bello and Olawuyi 2015). However, those hybrids of SCA significance positive effect for the traits indicated that dominance and epistasis were controlling the expression of the traits. SCA significance however allowed the characterization of deviating hybrid combinations to the mean parents' behaviour ((Meseka et al. 2006; Meseka and Ishaaq 2012).

Furthermore, exploitation of heterosis and selection of parents based on combining ability has been used as an important breeding approach in crop improvement had been reported by several researchers. Meseka et al. (2006) reported that preponderance of non-additive effects and positive heterosis for maize grain yield at low N production environments enable the advantage of hybrids exploitation under low N soil conditions. One of the efficient approaches in reducing cost of fertilizer is by developing high nitrogen use efficiency maize cultivars with superior grain yield potential. Again, the breeding for low N tolerant maize varieties is very important in enhancing maize productivity West and Central Africa. Based on the aforementioned, there is need to assess the genetic effects governing maize grain yield of different era in both high and low N conditions.This study was aimed (i) to identify the possible changes that might have occur in maize grain yield heterosis across two breeding eras, (ii) to compare cross combinations within and between two maize breeding eras that expressed highest heterosis across different environmental conditions and (iii) to investigate the nature of gene action involved in the expression of grain yield tested across different environments.

2 Materials and method

The plant materials used in this study comprised of ten open-pollinated varieties (OPVs) of maize, which were developed for grain yield and adaptation to biotic and abiotic stress factors at the International Institute of Tropical Agriculture (IITA), Ibadan. All of varieties were late maturing (approximately 120 days) and had white or yellow kernels. The materials were released in two different breeding eras. Those varieties that were released before year 2000 were classified as belonging to the first era (Era 1), while those that were released in year 2000 and above were considered as belonging to the second era (Era 2) as described in Table 1.

The ten OPVs were crossed in a partial diallel fashion to generate 45 F_1 hybrids during the 2011 cropping season at the IITA, Ibadan, Nigeria. The experimental hybrids were harvested, processed, fumigated and stored in the cold room prior to field evaluation. The 45 F_1 hybrids and the ten parents were evaluated in six environments in August, 2012. The two environments of research viz: Ikenne (Latitude 6^0 53^1N, Longitude 3^0 42^1E) and Ile-Ife (Latitude 7^0 18^1N, Longitude 4^0 33^1E) (rain forest region) were regarded as stress-free environments. Mokwa (Latitude 9^0 18^1N, Longitude 5^0N 4^1E) and Zaria

Table 1: Characteristics of ten maize varieties representing two Eras of maize breeding in Nigeria

S/N	Genotype	Era	Year of release	Grain colour	Endosperm Type	Maturity Rating	Breeding Emphasis
1.	TZSR-W-1	1	1979	White	Flint	Late	Tropically adapted and Streak virus resistance
2.	DMR-LSR-W	1	1980	White	Dent	Late	Downy mildew, low-N and Streak virus resistance/tolerance
3.	DMR-LSR-Y	1	1980	Yellow	Dent	Late	Downy mildew, low-N and Streak virus resistance/tolerance
4.	TZSR-Y-1	1	1979	Yellow	Flint	Late	Tropically adapted and Streak virus resistance
5.	ACR 99 TZLCOMP4 DMRSR	1	1999	White	Dent/Flint	Late	Tropical adapted, low-N and Downy mildew tolerance
6.	BR9922DMRSR	2	2008	White	Flint	Late	Borers, Downy mildew and Streak virus resistance.
7.	BR9928DMRSR	2	2008	Yellow	Flint	Late	Borers, Downy mildew and streak virus resistance.
8.	BR9943 DMRSR	2	2008	White	Flint	Late	Borers, Downy mildew and streak resistance
9.	AMATZBR-WC_2B	2	2008	White	Flint	Late	Tropically adapted and Borers resistance
10.	TZBRELD 4 C_0 W	2	2000	White	Flint	Late	Tropically adapted and Borer resistance.

Genotypes released before year 2000 = Era 1; Genotypes released in year 2000 and above = Era 2

(Latitude12^{0}00^{1}N, Longitude 8^0 22^{1}E) (Guinea savanna), which were the last four for nitrogen (N) study where the genetic materials were evaluated under high and low N conditions respectively. In all evaluations, two row plots were used. Each row was 6 m in length, spaced at 0.75 m between rows 0.25 m within rows with four replications to give a population density of approximately 53,333 plants per hectare. Observed cultural practices included pre-emergence spray of Gramozone and Primextra for weed control supplemented with hand weeding as necessary during the season. Fertilizer was also split applied using N-P-K 15:15:15 at ten days after planting (DAP) at the rate of 30 kg N/ha and top dressed with urea six weeks after planting at the same rate. However, the four locations at Mokwa and Zaria were the low and high-N environment with two different levels of nitrogen application (30 kg ha^{-1} and 90 kg ha^{-1}), respectively. Trials at Ibadan were separated into two equal halves of 3 m with a space of 1 m in the middle.

2.1 Statistical Analysis

2.1.1 Analysis of Combining Ability

Analysis of variance for each location across low-N and high-N were calculated with PROC GLM in SAS (SAS, 2012) first and later combined as a result of homogeneity of errors of variance with Levene's test. Hybrids were regarded as fixed effects while environments, replications and environments within replications were regarded as random effects. The sums of squares for hybrids x environments and hybrids were separated into sources of variation based on GCA and SCA and their interaction with environments (GCA x E and SCA x E), respectively, as described by Griffing's Model I and Method II of partial diallel analysis (Griffing 1956). The significance of sources of variation of GCA and SCA were evaluated utilizing the corresponding interaction with the environments as the error term. Significance of GCA x E and SCA x E were assessed employing pooled error. Adjusted means from PROC MIXED approach were also explored to determine SCA variance for the crosses and the GCA variance of the parents. The predicted performance of hybrids due to GCA was computed by adding the overall average grain yield of the hybrids to the GCA of parents. SCA and GCA were calculated using a fixed model of diallel. The relative importance of GCA and SCA was estimated as $[2MS_{GCA} / (2MS_{GCA}+MS_{SCA})]$. Where MS_{GCA} and MS_{SCA} are signify variance components of GCA and SCA, respectively (Baker 1978). The Percentage coefficient of variation (P<0.05) was exploited to calculate the degree of variation. Standard errors (SE) for all the genetic variances were determined using error mean squares from hybrids for the untransformed data.

Combining ability effect was computed as

$$g_i = 1/2n(Y_{i.} + Y_{.j}) - 1/n^2 Y.$$

Where: g_i = general combining effect of i^{th} line
n =number of lines involved in the cross
$(Y_i + Y_j)$ =sum of cross products from diallel table
Y = total sum of products from diallel table

Specific Combining Ability effect (SCA) effect was computed as

$$S_{ij} = ½ (Yij + YJi) - ½n (Yi + Yj + Yij) + Y.,$$

Where: S_{ij}= specific combining ability effect of a cross between $i^{th}$and j^{th} lines
Yij + Y_{ji} = sum of cross from diallel table
$Yi_{.} + Y_j + Y_{ij}$ =sum of cross products from diallel table
Y = Total of sum products from diallel table.

2.2 Estimation of Heterosis

High-parent or better and Mid-parent heterosis were calculated as described by Nadarajan and Gunasekaran 2008.

$$\text{Better parent heterosis \%} = \frac{F_1 \text{ - High parent value x 100}}{\text{High parent value}}$$

$$\text{Mid parent heterosis \%} = \frac{F_1 \text{ - Mid parent value x 100}}{\text{Mid parent value}}$$

Standard errors for high parent and mid-parent heterosis were estimated according to Nadarajan and Gunasekaran 2008.

$$Better - parent\ heterosis\ \% = \left(\frac{F_1 - Betterparent\ value}{Betterparent\ value}\right) \times 10($$

$$S.E. for\ mid - parent\ heterosis = \sqrt{\left(\frac{3}{2r} \times error\ mean\ square\right)}$$

Where *r* is number of replications.

The *t-test* values were determined to verify the significance of heterosis as described by Nadarajan and Gunasekaran, 2008.

Better-parent heterosis:

$$t_{calc} = \frac{F_1 - BP}{S.E}$$

Mid-parent heterosis:

$$t_{calc} = \frac{F_1 - BP}{S.E}$$

The estimates were significant whenever *tcalc* values were more than *ttabulated* values at 5% probability.

Ethical approval: The conducted research is not related to either human or animal use.

3 Results

Table 1 showed the mid- and high-parent heterosis for grain yield under stressed free environments. Highest and positive mid- and high-parent heterosis (67.87% and 63.49%) for grain yield were exhibited by hybrid DMR-LSR-Y (Era1) x BR9928DMRSR (Era 2) under stress free environment, while hybrids BR9922DMRSR x TZBRELD.4C_0W and ACR99T2LCOMP4-DMRSR x DMR-LSR-Y had the least positive mid- and high-parent heterosis (2.67% and 0.98%) for grain yield respectively under the same environment. Negative mid- and high-parent heterosis (-19.81% and -23.75%) were observed in hybrids DMR-LSR-W x TZSR-Y-1 and BR9922DMRSR x TZSR-W-1 respectively under stress-free environment. Mid-and high-parent heterosis across low-N environment are present in Table 2. The most positive percentages of mid-and high-parent heterosis (75.97% and 56.77%) were observed in hybrids DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) across low-N environment. However, hybrids DMR-LSR-Y (Era 1) x AMATZBR-WCZB (Era 2) and BR9922DMRSR (Era 2) x TZSR-Y-1 (Era 1) exhibited the least positive mid-and high-parent heterosis for grain yield under the same environments. Meanwhile, the highest negative mid-and high-parent heterosis (-9.03 and -12.72) were recorded by hybrids TZSR-W-1 (Era 1) x BR9922DMRSR (Era 2) and BR9943 DMRSR (Era 2) x BR9922DMRSR (Era 2).

3.1 Combined analysis of variance

Combined ANOVA across the two locations indicated that the mean squares of environments and interaction between Hybrids × environments were significant (P <0.01) at low-N, High-N and across both environments (Table 3). Hybrids, GCA and SCA were significant at high-N and across both environments, but not at low-N. However, GCA x E and SCA x E were significant at all the environments. The Baker ratio of GCA to SCA was greater than unity at all the environments.

Table 3 shows the mid-and high-parent heterosis for high-N environment for grain yield. The most positive values of mid-and high-parent heterosis (97.7 and 87.15%) were manifested by hybrid DMR-LSRW (Era 1) x TZSR-Y-1 (Era

Table 2: Combined analysis of variance for grain yield in F1 hybrids and parents under low-N and high-N at Mokwa and Zaria in 2012

Source of variation	Df	Low-N	High-N	Across both environments
Environments (E)	3	95.34**	101.72**	98.56**
Reps (E)	12	0.11	0.38	0.37
Hybrids	44	0.08	17.54**	9.89**
GCA[a]	9	0.66	11.89**	10.72**
SCA[a]	44	0.56	18.35**	11.33**
Hybrids x E	132	11.91**	20.15**	18.83**
GCA x E	27	2.45*	31.66**	29.66**
SCA x E	132	54.18**	3.56*	48.01**
Residual error	206	0.54	1.63	1.58
GCA/ SCA				
CV %				

*, ** Significant at P=0.05 and P=0.01, respectively

[a] GCA x E was used to test the significance of MS for GCA

[b] SCA x E was used to test the significance of MS for SCA

Table 3: Mid-parent heterosis (upper diagonal) and high-parent heterosis (lower diagonal) for maize grain yield under low-N conditions at Mokwa and Zaria, 2012

	TZSR-W-1	DMR-LSR-W	DMR-LSR-Y	TZSR-Y-1	ACR9922TZ LCOMP4-DMRSR	BR9922 DMRSR	BR9928 DMRSR	BR9943 DMRSR	AMATZBR-WC2B	TZBRELD .4C0-W
TZSR-W-1	_	-0.46	9.40	9.58	19.51	-9.03	53.71	21.55	26.36	11.9
DMR-LSR-W	-2.76	_	14.91	9.26	22.79	23.62	75.97	24.82	8.96	11.45
DMR-LSR-Y	5.29	13.17	_	30.53	23.79	19.03	37.28	16.65	2.85	24.85
TZSRY1	7.74	4.99	23.6	_	61.05	4.40	33.25	50.17	31.1	17.57
ACR99TZLCOMP4-DMRSR	11.5	17.2	19.92	48.01	_	20.03	70.41	34.06	45.28	23.25
BR9922DMRSR	-4.56	15.48	9.63	1.38	7.39	_	52.88	15.56	28.99	68.28
BR9928DMRSR	34.16	56.77	53.78	14.64	55.48	12.25	_	55.55	56.17	42.17
BR9943DMRSR	8.9	14.24	26.44	32.56	28.25	-12.72	51.01	_	37.21	40.91
AMATZBR-WC2B	20.71	1.79	-5.27	27.31	40.23	15.41	31.1	18.07	_	31.49
TZBRELD.4C0W	10.92	9.81	21.18	14.61	16.00	41.71	36.5	27.23	24.57	_

1) under high-N environment. However, the lowest positive percentages of mid-and high-parent heterosis (0.16% and 1.5%) were recorded for hybrids ACR9922TZLCOMP-DMRSR x TZBRELD.4.C0W and TZBRELD.4.C0W x BR 9943 DMRSR under high-N environment. Hybrids DMRLSR-W (Era 1) x AMATZBR-WC2B (Era 2) had negative percentages of mid-and high-parent heterosis (-14.96% and -27.81%) under low-N environment.

Parent DMR-LSR-W obtained the highest values of the estimate of GCA effects for grain yield under natural field condition at Ikenne and Ife (Table 4). However, all other parents had low and negative GCA effect across the environments. Maize grain yield assessment under natural field condition showed that DMR-LSR-W combined well with TZSR-W-1, DMR-LSR-W, TZSR-Y-1, TZSR-W-1, ACR99TZLCOMP-4DMRSR, BR9922DMRSR, BR9928DMRSR, BR9943DMRSR, AMATZBR-WC$_2$B and TZBRELD.4C$_0$W. All other cross combinations had low and non-significant effects for grain yield under natural field environment.

Yield assessment in low nitrogen application environment revealed highest but non-significant GCA effects for grain yield in parent AMATZBR-WC$_2$B (Table 5). All other parents had low and non-significant GCA effects. The cross combinations TZSR-W-1 x BR9922DMRSR, TZSR-W-1 x AMATZBR-WC$_2$B, DMR-LSR-W x BR9922DMRSR, DMR-LSR-W x BR9928DMRSR, DMR-LSR-W x TZSR-W-Y, TZSR-W-Y x ACR99TZLCOMP-4DMRSR, ACR99TZLCOMP-4DMRSR x BR9922DMRSR, ACR99TZLCOMP-4DMRSR xAMATZBR-WC$_2$B, BR9928DMRSR x AMATZBR and BR9943DMRSR x TZBRELD.4C$_0$W had high but non-significant values of SCA for grain yield across low-N environments.

Table 4: Mid-parent heterosis (upper diagonal) and high-parent heterosis (lower diagonal) for maize grain yield in high-N environment at Mokwa and Zaria, 2012

	TZSR-W-1 TZSR-W-1	DMR-LSR-W	DMR-LSR-Y	TZSR-Y-1	ACR9922TZ LCOMP4-DMRSR	BR9922 DMRSR	BR9928 DMRSR	BR9943 DMRSR	AMATZBR-WC2B	TZBRELD .4C0-W
TZSR-W-1	_	24.6	51.15	41.19	3.98	3.52	56.24	59.01	7.49	19.12
DMR-LSR-W	20.7	_	53.59	97.7	27.91	42.27	71.18	61.57	-14.96	42.73
DMR-LSR-Y	48.79	51.11	_	52.61	21.97	9.68	70.67	15.76	6.36	20.92
TZSR-Y-1	29.72	87.15	42.27	_	39.87	50.24	77.1	47.06	40.39	17.02
ACR99TZLCOMP4-DMRSR	-3.77	14.99	11.27	19.7	_	32.12	60.5	38.48	31.42	0.16
BR9922DMRSR	-2.81	26.42	-1.12	27.28	30.41	_	46.3	46.04	9.35	47.85
BR9928DMRSR	38.18	55.78	53.05	69.83	32.76	19.77	_	96.47	30.01	8.41
BR9943DMRSR	53.9	51.65	10.34	31.15	32.22	37.72	68.89	_	16.28	11.65
AMATZBR-WC2B	-6.26	-27.81	26.95	13.95	-3.75	3.75	2.19	4.38	_	40.7
TZBRELD.4C0W	5.15	22.58	5.29	-3.98	-4.87	42.15	13.65	1.5	42.7	_

Table 5: General and Specific combining ability (GCA and SCA) for maize grain yield across Low-N environment (Mokwa and Zaria, 2012)

Genotype	DMR-LSR-W	DMR-LSR-Y	TZSR-Y-1	ACR9922TZ LCOMP4-DMRSR	BR9922 DMRSR	BR9928 DMRSR	BR9943 DMRSR	AMATZBR DMRSR	TZBRELD .4C0-W .	GCA
TZSR-W-1	-0.15	0.03	-0.06	-0.01	-0.28	0.36	0.09	0.23	-0.04	-0.10
DMR-LSR-W		0.06	-0.13	-0.03	0.24	0.61	0.07	-0.15	-0.11	-0.08
DMR-LSR-Y			0.24	-0.01	0.17	0.04	-0.04	-0.25	0.12	-0.12
TZSR-Y-1				0.52	-0.19	-0.09	0.40	0.17	-0.09	0.08
ACR99TZLCOMP4-DMRSR					-0.03	0.28	-0.003	0.27	-0.12	0.04
BR9922DMRSR						0.05	-0.26	0.003	0.61	0.03
BR9928DMRSR							0.12	0.27	0.02	0.05
BR9943DMRSR								0.2	0.22	-0.12
AMATZBR-WC2B									0.15	0.16
TZBRELD.4C0W										0.05

*,** Significant at < 0.05 and 0.01 levels of probability respectively.

Non-significant positive GCA effect for grain yield across high-N environments was obtained in parent BR9922DMRSR, while GCA effects for other parents were negative and non-significant (Table 6). However, significant and positive SCA for grain yield were observed in cross combinations TZSR-W-1 x BR9928DMRSR, TZSR-W-1 x BR9928DMRSR, TZSR-W-1 x BR9943DMRSR, DMR-LSR-W X DMR-LSR-Y, DMR-LSR-W X ACR99TZLCOMP4-DMRSR, DMR-LSR-Y x ACR99T2LCOMP4-DMRSR, TZSR-Y-1 x TZSR-W-1 BR9928DMRSR, TZSR-Y-1 x BR9928DMRSR, BR9943DMRSR x AMATZBR-WC2B and BR9943DMRSR x TZBRELD.4C_0W across High-N environment.

4 Discussion

4.1 Combined analysis of variance

Highly significant mean squares of environments and hybrids × environments interaction obtained in all the environments signified differences in OPVs performance as parents in hybrid combinations. High GCA significant effect obtained in this study showed the *per se* performance of the parents. This also indicated the preponderance of additive gene action and genetic

Table 6: General and Specific combining ability (GCA) and (SCA) for grain yield under high-N environment at Mokwa and Zaria, 2012

Genotype	DMR-LSR-W	DMR-LSR-Y	TZSR-Y-1	ACR9922TZ LCOMP4-DMRSR	BR9922 DMRSR	BR9928 DMRSR	BR9943 DMRSR	AMATZBR-WC2B	TZBRELD .4C0-W	GCA
TZSR-W-1	0.02	0.02	-0.33*	-0.71**	0.54**	0.38*	0.31*	0.21	0.002	-0.15
DMR-LSR-W		0.27*	0.16	0.29*	-0.21	-0.12	0.06	0.21	0.25*	-0.03
DMR-LSR-Y			0.17	0.04	0.04	0.13	0.06	-0.04	-0.24*	-0.15
TZSR-Y-1				-0.06	-0.06	0.27*	0.21	0.11	-0.10	-0.03
ACR9922TZLCOMP4-DMRSR					0.06	0.15	0.09	0.23	-0.23	0.04
BR9922DMRSR						-0.1	-0.16	-0.52**	0.27*	0.10
BR9928DMRSR							-0.33	0.31	-0.144	-0.03
BR9943DMRSR								0.25	0.29*	0.08
AMATZBR-WC2B									-0.06	0.05
TZBRELD.4C0W										0.11

*,** Significant at < 0.05 and 0.01 levels of probability respectively.

diversity of the parents. This will allow selection of crosses with outstanding GCA with better performance. Nonetheless, significance SCA at high-N and across both environments indicated predominant dominance and epistasis effects. Comparatively, the ratio GCA to SCA estimate was more than one, showing a predominance of GCA in the expression of all characters and also governed by additive genetic action.

4.2 Heterosis estimates

Heterosis for grain yield being the most important economic traits of maize was studied in other to identify populations that may be useful sources for inbred line development and base populations for recurrent selection. According to Kiani et al. (2015), greater success should be expected when inbred lines are developed from populations which show substantial heterosis in crosses. Under low-N condition, mid and high parent heterosis for grain yield were 29.14 and 19.81% respectively, which is similar to values obtained by Fakorede (1984), who reported 35 and 19% for grain yield mid and high-parent heterosis in the study conducted in 20 different environments in Nigeria. Furthermore, mid and high-parent heterosis for hybrids under high, stress free and optimum N-fertilizer environments were 37.20% and 25.38%, 30.98% and 18.94% respectively. These results except values obtained under optimum N condition still fell within the same range with the earlier report by Fakorede (1984). Cross combination DMR-LSR-W (Era 1) x TZSR-Y-I (Era 2) expressed the highest magnitude of mid and high-parent heterosis (97.70% and 87.15%) for grain yield under high-N and across the other four test environments., However, the same hybrid expressed very low mid and high-parent heterosis (9.26% and 4.99%) under low-N environment, which suggest that the suitability of the hybrid for cultivation only in environments with high productivity index.

As it is accentuated, grain yield is a complex character that is conditioned on plant and environment interaction starting from the day of planting to harvest. Furthermore, being quantitative character, it is controlled by many genes with individual contributing little additional effect on the total expression. Moreover, heterosis expressed by the hybrids mainly dependent on the genetic diversity of the parental genotypes used (Telebi 2010). Thus, this suggests that low heterosis of grain yield is a resultant closeness of OPVs used in this research. A study conducted by Betran et al. (2003) to determine relationship between genetic diversity and heterosis in tropical maize under stress environment, observed that SCA had the strongest correlation with genetic diversity, and that the environment significantly affected the correlation between F_1, SCA, mid- and high-parent heterosis. In this study, cross combinations DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) and ACR99TZLCOMP4DMRSR (Era 1) x BR9928DMRSR (Era 2) under low-N, DMR-LSR-Y (Era 1) x BR9928DMRSR (Era 2) and BR9928DMRSR (Era 2) x BR9943DMRSR (Era 2) had high heterosis under stress-free condition for grain yield. Positive heterosis for this character has been reported by several workers (Amiruzzaman et al. 2011; Jain and Bharadwaj 2014), while Rozende and Souza (2000) observed low heterosis. for grain yield. Incidentally, these hybrids were derived mostly from crosses between Era 1 x Era 2 genotypes, which still show the extent of genetic diversity between the maize genotypes from the two breeding eras. This result was in line with earlier findings of Moll et al. (1965) who reported that the heterosis manifested by crosses depends on genetic divergence of two parental varieties. Therefore, these crosses hold promise as future candidates for commercial exploitation of heterosis or for the extraction of inbred lines, to derive and isolate lines with gene combination for high grain yield. Moreover, the cross combinations DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) (under stress free), DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) (under low-N) that recorded excellent heterosis for grain yield could effectively be exploited in similar hybrid breeding programmes.

It is noteworthy that the heterosis estimate is character specific. therefore, to comprehend the heterosis mechanisms research should be carried out and inferred on the specific characters (Kaeppler 2012). Banerjee and Kole (2011) and Jain and Bharadwaj (2014) opined that the crosses that revealed high heterosis could be explored to develop superior genotypes that for hybridization programs. As revealed in this study, in most cases inter-era cross combinations manifested better heterosis than cross combinations within maize breeding eras. This is an indication that individual maize genotypes belonging to Eras 1 of breeding complement those in Era 2 to produce better heterosis among the ten maize populations. This also implies that changes in breeding objectives have also altered the magnitude of heterosis in newer maize varieties. Backcrossing to the older varieties is suggested for the restoration of original magnitude of heterosis in the modern maize varieties.

General and specific combining ability estimates

Parent DMR-LSR-W (Era 1) obtained the highest values of the estimate of GCA effects for grain yield under natural field condition at Ikenne which according to Aminu et al. (2014), means that it is capable of producing superior segregants in the F_2 as well as in later generations and as such, could be utilized as parents in a hybridization programme for the selection of superior recombinants. Parent AMATZBR-WC$_2$B with higher GCA effects and mean values for grain yield, and cross combinations DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) and BR9922DMRSR (Era 2) x TZBRELD-4C$_0$W (Era 2) with higher SCA for grain yield under low-N environment on the other hand, are promising candidates for the development of nitrogen use efficient varieties for cultivation in low-N environments. Moreover, cross combinations within more recent Eras, and between older and modern maize varieties are good sources of genes for the development of low-N tolerant maize varieties for low-N environments. Parent TZBRELD-4C$_0$W (Era 2) on the other hand, was the best general combiner for grain yield and simultaneously possessed high mean values under high-N environment and so could be used in the extraction of productive inbred lines for use in hybrid breeding programmes with a view to increase the yield level. It also an indication that the modern maize varieties combined well with other lines for grain yield under adequate supply of nitrogen relative to older varieties. Kumar et al. (2012) noted that maximum gain from selection could be achieved by maintaining considerable heterozygosity, coupled with selection in the segregating generation to enhance recombination which might result in breaking of undesirable linkage. According to the authors, this will likely ensure accumulation of transgressive segregants for the expression of maximum number of potentially functional genes for the improvement of the traits leading to production of stable and widely adapted genotypes. These parental lines and cross combinations are promising sources of genes for future hybrid development programmes in the tropical African region.

5 Conclusion

The recent OPVs of 2000 breeding era were very productive with the older varieties, irrespective of the quantity of N fertilizer applied to the soil. Under low-N condition, mid and high parent heterosis for grain yield were low indicating the suitability of the hybrids for cultivation only in environments with high productivity index. Hybrid DMR-LSR-W (Era 1) x TZSR-Y-I (Era 2) had greatest mid and high-parent heterosis for grain yield under high-N and across the other four test environments. Parent AMATZBR-WC$_2$B with higher GCA effects and mean values for grain yield, and cross combinations DMR-LSR-W (Era 1) x BR9928DMRSR (Era 2) and BR9922DMRSR (Era 2) x TZBRELD-4C$_0$W (Era 2) with higher SCA for grain yield under low-N environment on the other hand, are promising candidates for the development of nitrogen use efficient varieties for cultivation in low-N environments.

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References

Acquaah G., Principles of plant genetics and breeding. Blackwell Publishing, USA, 2012

Amiruzzaman M., Islam M.A. Pixel K.V., Rohman M.M., Heterosis and combining ability of CIMMYT's tropical × sub-tropical quality