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GENETIC GAINS IN THREE BREEDING ERAS OF MAIZE HYBRIDS UNDER LOW AND OPTIMUM NITROGEN FERTILIZATION

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Abstract: A comparative study on the response of six maize hybrids: two hybrids each from the 1980s (8321-21 and 8425-8), 1990s (9801-11 and 9803-2) and 2000s (0103-11 and 0103-15) to sub-optimal and optimal nitrogen fertilization was conducted in Oke-Oyi, Nigeria. The trials were set up in a split plot with three nitrogen levels (0, 30 and 90 kg N ha^{-1}) as a main plot and six hybrids as sub-plots. Significant interactions were observed between hybrid and N level for all characters, with increasing in variation as the level of N decreased. Mean grain yield reductions across eras were 73.8% at no-N and 32.6% at low-N, and those of optimal-N fertilization were 34.3% and 15.7% for 1980s and 1990s genotypes respectively. Depending on N treatment, grain yield varied from 0.67 to 4.89 t ha^{-1}. Kernel number was most severely reduced by N stress, but had positive and highly significant ($p \leq 0.01$) correlation with grain yield at all N levels. Genetic gains in grain yield were 42% (between 1980 and 2000 eras) and 9% (between 1990 and 2000 eras) under optimal-N fertilization. The two modern hybrids of 2000 era (0103-11 and 0103-15) were outstanding for all the agronomic traits and leaf chlorophyll concentration at all N levels. Improving traits associated with fertilizer N response could accelerate rate of genetic gains in maize yields.

Key words: anthesis, grain yield, kernels, N stress, plant height.

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Introduction

Comparisons of maize cultivars over decades (eras) are common approaches to understand how genetic selection has influenced grain yield in maize (Campos et al., 2006; Wang et al., 2011). Efforts to improve maize adaptation to low soil fertility have been documented (Meseka et al., 2006; Emede and Alika, 2012; Jason et al., 2013). Maize cultivars exhibited differential response for grain yield at low and high nitrogen (N) fertilizer applications (Lafitte and Edmeades, 1994; Agrama et al., 1999). O'Neill et al. (2004) reported that most recent maize hybrids had superior grain yield response to applied N and greater N fertilizer use efficiency compared to older hybrids. In comparative studies of twenty-five open-pollinated and hybrid maize cultivars performed between the 1930s and 1980s, Castleberry et al. (1984) reported that genetic gains for grain yield under low and high soil fertility were 51 and 87 kg ha^{-1} year^{-1} respectively. Similarly, among four hybrids representing Brazilian maize germplasm released between 1960s and 1990s, the most recent maize hybrids produced higher grain yields at all levels of N (Sangoi et al., 2001). Likewise, a newer hybrid (Pioneer 3902, released in 1988) produced approximately 25% grain yield advantage than an older hybrid (Pride 5, released in 1959) at both low and high N levels (Tollenaar et al., 1997). O'Neill et al. (2004) reported that progress has been made in improving maize grain yield under low and high N fertilization, but characterization of changes in the agronomic and physiological components of maize in soil N utilization could also identify strategies for continued genetic improvement of yield.

In Nigeria, maize improvement for grain yield and secondary traits including the use of artificial fertilizers on hybrids and adoption of improved agro-technical production systems has gone through several stages since 1950 (Adebo and Olaoye, 2010; Emede and Alika, 2012; Abe et al., 2013). Development and release of maize cultivars for different agro-ecologies started with introgression of genes for high grain yield, pest and disease resistance (Kim et al., 1993; Fakorede et al., 1993; 2001; Olaoye, 2009) to adaptation to different ecologies and stress factors (Kim, 1997). By the year of 1962, estimated gains in grain yield were between 1.5 and 2.5 t ha^{-1} (43.71%) approximating 1.4 to 2.4% gains per year from 1950 (Fakorede et al., 1993). However, research on the use of hybrids in Nigeria commenced in the early 1970s (Fakorede et al., 1993) and became an integral part of the Maize Improvement Program at the International Institute of Tropical Agriculture (IITA) in 1979 (Kim, 1997). Experimental hybrids were tested on farmers' fields located across the country in 1984 (Fakorede et al., 1993). Between 1985 and 1990, open pollinated varieties (OPVs) and hybrid improvement resulted in further yield increase from 4.25 to 5.15 t ha^{-1}, representing an average of 22% yield advantage for the hybrids (Kim et al., 1993). Many commercial hybrids were therefore developed and marketed by the seed companies. Since then, maize grain yield has been increased to about 14.7 t ha^{-1} in high yielding environments, especially in the research stations, representing 20% to 40% yield advantage (Kim, 1997). Genetic gain in grain yield was about 0.41% per year between 1970 and 1999 (Kamara et al., 2004), and 24% yield advantage between 1970s and 1990s hybrid cultivars (Adebo and Olaoye, 2010). This yield increase was attributed to genetic improvement in the crop, effective management practices, high plant densities, weed interference as well as high tolerance of the hybrids to low soil moisture and N stresses (Tollenaar et al., 1997; Duvick and Cassman, 1999; Tollenaar and Wu, 1999; Olakojo et al., 2005).

Average maize yield on the farmers' farm is still low (1.78 t ha^{-1}) in the savannas of West and Central Africa including Nigeria because cultivation is carried out under conditions of low soil fertility coupled with inherent erratic and unreliable amount and distribution of rainfall, low soil nutrient status and water holding capacity, thereby causing fragility of the soil that is consistently prone to drought (FAOSTAT, 2010; Bello et al., 2011). The resource-poor farmers applied sub-optimal N fertilizer (8 kg of N/ha) due to high price ratios between fertilizer and grain, limited availability of fertilizer, and low purchasing power of farmers (Abe et al., 2013; Bello et al., 2014). Sub-optimal N fertilizer regimes therefore have resulted in low yield of maize hybrids in Africa (Worku et al., 2007; Abe et al., 2013). Thus, development and adoption of maize cultivars with improved grain yield under low and optimal soil N could be beneficial to low-input agriculture. The objective of this study was to evaluate the performance of six maize hybrids developed in the Nigerian Savanna during the past 20 years at sub-optimal and optimal levels of N fertilizer applications.

Material and Methods

Field experiments were carried out at the Lower Niger River Basin Development Authority station (8°30'N, 8°36'E and 945 m above sea level) located in the southern Guinea savanna agro-ecology of Nigeria. The soil is classified as Typic Paleustalf (United States Department of Agriculture, USDA soil taxonomy). Six maize hybrids developed and widely tested in Nigerian savanna from 1982 to 2000 were used in this study; two hybrids each from the 1980s (8321-21 and 8425-8), 1990s (9801-11 and 9803-2) and 2000s (0103-11 and 0103-15).

Prior to sowing in the evaluation site in each year, top soil samples were collected at random from a depth of 0–15 and 15–30 cm for physical and chemical analyses. Twenty core samples collected randomly were mixed inside a plastic bucket and a composite sample was thereafter taken. The samples were air-dried, crushed and sieved through a 2-mm sieve. Samples were analyzed in the laboratory for some physical and chemical properties using the procedures described in the laboratory manual of the International Institute of Tropical Agriculture

(IITA, 1979). Particle size distribution was carried out by hydrometer method while soil pH was measured with the glass-electrode pH meter on 1:1 soil solution mixture. The total nitrogen (N) and available phosphorus (P) were determined by Macro-Kjeldahl and Bray-1 method respectively. The organic carbon was determined by Walkey-Black method while the exchangeable cations were extracted with 1 N NH_4OAc solution. Potassium (K), calcium (Ca), and sodium (Na) were measured using the flame photometer, and magnesium (Mg) was determined by the atomic absorption spectrophotometer. Exchangeable acidity (H^+) of the soil was determined by titration method. Effective cation exchange capacity (ECEC) was established as the sum of exchangeable cations K, Na, Ca, Mg and H^+ expressed in cmol kg^{-1} of soil. Base saturation was calculated with reference to NH_4OAc-CEC. The results of the analyses are shown in Table 1. Rainfall distribution and temperature data for 2012 and 2013 cropping years were also obtained from the Meteorological Department, Lower Niger River Basin Development Authority, Ilorin, Nigeria (Table 2).

Table 1. Physico-chemical characteristics of the soil in the experimental site prior to maize cropping at Ilorin, Nigeria in 2012 and 2013.

Soil properties	0–15 cm depth		15–30 cm depth	
	2012	2013	2012	2013
Physical characteristics (g kg^{-1})				
Sand	73.1	73.0	73.0	73.1
Clay	5.8	5.9	5.8	5.8
Silt	20.1	20.0	20.0	20.0
Textural class	Sandy loam	Sandy loam	Sandy loam	Sandy loam
Chemical characteristics				
Soil pH (H_2O)	6.3	6.2	6.3	6.3
Organic carbon (g kg^{-1})	8.4	8.3	8.3	8.3
Total nitrogen (g kg^{-1})	0.6	0.6	0.6	0.6
Available phosphorus (mg kg^{-1})	6.1	6.2	6.1	6.1
Exchangeable bases (cmol kg^{-1})				
Ca	1.4	1.5	1.4	1.4
Mg	1.4	1.3	1.4	1.4
Na	0.19	0.18	0.19	0.19
K	0.30	0.30	0.30	0.30
Exchangeable acidity H^+ (cmol kg^{-1})	1.1	1.1	1.1	1.1
ECEC (cmol kg^{-1})	11.8	11.9	12.11	12.12
Base saturation (g kg^{-1})	16.4	16.3	16.3	16.3

Soil texture of the experimental site in 2012 and 2013 cropping seasons was sandy loam (Table 1). The nutrients determined in both years were the same, with slightly lower values for base saturation in 2012. The soil acidity was however higher in 2012. The years of 2012 and 2013 represented two different environments for evaluating agronomic characters and N use traits (Table 2).

There was little variation in temperature in both years and they were generally cooler than average, particularly at flowering and during grain filling in September. The average monthly rainfall showed marked variation in both years ranging from 0 to 201 mm in November and September respectively. The average rainfall during planting in July, 2012 was higher compared to 2013, whereas at harvest in October, 2012 the average rainfall was lower.

Table 2. Rainfall and temperature at the experimental site in 2012 and 2013 cropping years.

Month	Temperature (°C)				Rainfall (mm)	
	2012		2013			
	Min	Max	Min	Max	2012	2013
June	21	30	21	30	162.8	132.9
July	21	28	22	28	202.7	106.8
August	21	27	21	27	168.7	17.7
September	22	27	22	29	200.8	200.7
October	21	30	22	31	52.8	150.6
November	22	33	23	35	0	0
December	19	34	21	34	7.2	11.4

A split-plot factorial experiment in a randomized complete block design with four replications was used in each year. The main plot treatments consisted of three N fertilization rates (0, 30, 90 kg N ha^{-1}). The sub-plot comprised of six maize hybrids. The sub-plots dimensions were 3 × 5 m^2 and consisted of four rows with 0.75 m of spacing between rows and 0.25 m within row.

The experimental field was cleared, ploughed, harrowed and ridged. Planting was carried out on the 18th July, 2012 and the 25th July, 2013. Two seeds were planted per hill and later thinned to one to obtain a plant population density of 53,333 plants per hectare. The inner two rows in each plot were used for yield determination and the outer two rows served as borders. At planting, the experiments in the two-year period received basal application of P in form of single super phosphate and K as muriate of potash at the rate of 60 kg P_2O_5 ha^{-1} and 30 kg K_2O ha^{-1} respectively. N fertilizer in form of urea was applied in two equal split doses, the first half at 2 weeks after planting (WAP) and the second dose at 4 WAP. The trials were kept weed-free using herbicides (3 kg/l of Metolachlor, 170 g/l of Atrazine and 3 kg/l of Paraquat per hectare) and complemented with hand weeding.

Days to anthesis and silking were calculated as the number of days from planting to when 50% of the plants shed pollens and extrude silks respectively. Anthesis-silking interval was expressed as the interval in days between silking and anthesis. Plant height was measured in meters as the distance from the base of the plant to the height of the first tassel branch. In all trials, *in vivo* chlorophyll concentration of the ear leaf was assessed two weeks after male flowering and each following two weeks, on 10 plants, using a portable chlorophyll meter (SPAD-502, Minolta, Tokyo, Japan), expressed in arbitrary absorbance (SPAD) values (Dwyer et al., 1991). Since chlorophyll content in a leaf is closely correlated with leaf N concentration (Blackmer and Schepers, 1995), the measurement of chlorophyll provides an indirect assessment of leaf N status. The number of ears plant^{-1} was calculated as the proportion of total number of ears divided by the number of plants harvested. The number of kernels was recorded as the number of kernels on ear per plant after shelling. One thousand-kernel weight was measured in gram as the weight of 1,000 kernels adjusted to 12.5% moisture content. All ears harvested from each plot were shelled to determine percentage moisture, and grain yield adjusted to 12.5% moisture was computed from the shelled grain weight.

Statistical analysis was performed on all measured traits using the SAS for Windows Release 9.2 (SAS Institute, 2009). The SAS GLM procedure used for the ANOVA was mixed model. Replication was treated as a random effect, while nitrogen rate and hybrids as fixed effects. Differences between two treatment means were compared using Least Significant Difference (LSD). Pearson's correlation coefficient was used to test for an association between grain yield and other variables at each N level using PROC CORR of SAS.

Results and Discussion

Analysis of variance and flowering traits

Analysis of variance of the two-year data showed significant differences among cultivars, N rates and nitrogen × hybrids interaction for grain yield and other yield components (Table 3). Regardless of N rate, days to anthesis were consistently lower in newer 2000s hybrids than in the hybrids that preceded them (Table 4). Silk delay due to N stress varied with hybrids, and was not consistent between the old and new hybrids. N stress with no-N fertilization (0 kg N ha^{-1}) delayed days to silking by 8 days. Hybrids 84218 of 1980 era recorded days to silking that were significantly higher than those of earlier decades. Severed N stress however affected anthesis-silking interval (ASI) negatively and was reduced with increasing N rates for all hybrids evaluated. All hybrids recorded statistically similar ASI except older 1980s hybrid, 84218 which had (5 days) ASI higher than the other hybrids under severed N stress. ASI did not significantly differ among hybrids at low-N (30 kg N ha^{-1}). Under optimal-N fertilization (90 kg N ha^{-1}) newer 2000s hybrids (0103-15) recorded the lowest ASI (one day). Excessive silk delay is a predictor of barrenness and the production of fewer kernels per ear (Sangoi et al., 2001). This agronomic feature allowed the newest hybrid to set more kernels per plant, contributing to its grain yield superiority over the older genotypes.

Table 3. Interactive effects of year (Y) × nitrogen (N) × hybrids (H) on variance of agronomic response of six maize hybrids to varying N fertilization.

Source	Days to anthesis	Days to silking	Anthesis-silking interval	Plant height	Ear leaf chlorophyll content	Number of ears plant^{-1}	Number of kernels	1000-seed weight	Grain yield
Replication	3.4	7.3	0.5	1.5	9.7	9.3	1.1	5.3	4.7
Y	0.3	12.1	12.6	11.4	4.7	11.9	10.3	13.4	0.7
SE	0.1	4.1	1.6	10.8	11.8	12.7	10.3	0.1	11.4
N	235.7^{**}	235.3^{**}	126.8^{*}	134.7^{*}	103.4^{*}	140.1^{*}	314.3^{**}	267.6^{**}	153.9^{*}
Y × N	2.6	11.5	12.5	2.3	7.6	10.1	11.2	0.7	220.4^{**}
SE	12.4	4.6	10.2	9.3	11.7	10.1	7.3	0.6	12.7
H	173.3^{**}	103.6^{*}	231.3^{*}	122.1^{*}	123.3^{*}	131.7^{*}	100.1^{*}	123.7^{*}	111.3^{*}
Y × H	2.4	5.2	1.2	2.7	7.4	2.2	0.5	4.0	1.2
N × H	123.4^{*}	124.8^{*}	110.5^{*}	215.5^{**}	130.4^{*}	210.8^{**}	210.8^{**}	314.8^{**}	210.64^{**}
Y × N × H	10.3	11.6	3.6	17.3	16.3	13.6	0.9	1.5	0.6
SE	0.4	11.7	0.7	8.3	10.9	11.6	10.3	13.2	11.3
CV (%)	4.6	11.4	23.6	4.8	26.2	11.9	2.8	5.4	30.2

*, ** Significant at the 0.05 and 0.01 probability levels respectively. SE = Standard error, CV = Coefficient of variation.

Table 4. Anthesis-silking interval, days to anthesis and silking of six maize hybrids of three breeding eras under varying N fertilization at Oke Oyi, Ilorin, Nigeria in 2012 and 2013.

Parameters		Days to anthesis				Days to silking				Anthesis-silking interval (days)			
Nitrogen (kg ha^{-1})		0	30	90	Across N	0	30	90	Across N	0	30	90	Across N
Year													
2012		61	57	55	57.6	65	60	57	60.7	4	3	2	3.0
2013		61	57	55	57.6	65	61	57	61.0	4	4	2	3.3
SE		3.4	10.7	7.3	7.1	3.7	7.7	11.5	7.6	10.2	3.9	5.4	6.5
Hybrid	*Era*												
0103-11	2000	60	56	54	56.6	64	59	56	59.7	4	3	2	3.0
0103-15	2000	60	55	54	56.3	63	58	55	58.7	3	3	1	2.3
9801-11	1990	62	56	55	57.6	66	59	57	60.7	4	3	2	3.0
9803-2	1990	61	58	55	58.0	65	61	57	61.0	4	3	2	3.0
8321-21	1980	61	58	56	58.3	65	61	58	61.3	4	3	2	3.0
84218	1980	62	59	56	59.0	67	63	58	62.7	5	4	2	3.0
Mean		61	57	55		65	60	57		4	3	2	
SE		10.5	7.8	11.5	9.9	11.4	10.1	9.8	10.4	6.7	4.9	11.7	7.8
$\text{LSD}_{(0.05)}$		ns	ns	ns	ns	2,4	1,3	1.4	2.5	1.5	ns	ns	ns

SE = Standard error.

Fewer days to silking and shorter ASI among the 2000-era hybrids demonstrate that loss of synchrony between male and female inflorescences was less pronounced in the modern hybrids under severed N stress. Sangoi et al. (2001) also reported similar results for Brazilian hybrids.

The lack of difference among most hybrid cultivars under severed N stress suggests that ASI in these cultivars responded similarly to N stress. The higher mean of ASI under no-N fertilization corroborates the findings of Kamara et al. (2012) that severed N stress increases ASI in maize. Jason et al. (2013) also observed that selection against silk delay has been considered as one of the most effective breeding methods to improve maize tolerance to environmental stresses.

Plant height, number of ears per plant and ear leaf chlorophyll concentration

The hybrids of the 1980 and 1990 breeding eras had lower percentage of plant height, ear leaf chlorophyll concentration and number of ears plant^{-1} than the most recently introduced hybrids (Table 5). Severed N stress with no-N fertilization stimulated barrenness in all the hybrids evaluated. Older hybrids recorded lower number of ears plant^{-1} than the newer ones.

Table 5. Plant height, number of ears plant^{-1} and ear leaf chlorophyll content of six maize hybrids of three breeding eras under varying N fertilization at Oke Oyi, Ilorin, Nigeria in 2012 and 2013.

Parameters		Plant height (cm)				Ear leaf chlorophyll content (SPAD)				Number of ears plant^{-1}			
Nitrogen (kg ha^{-1})		0	30	90	Across N	0	30	90	Across N	0	30	90	Across N
Year													
2012		99	147	153	133.0	19.6	31.9	40.5	36.7	0.69	0.81	1.03	0.84
2013		101	145	153	133.0	19.7	31.8	40.9	30.8	0.67	0.81	1.04	0.84
SE		11.7	8.3	12.1	10.7	11.2	3.7	8.4	7.8	6.8	10.3	11.6	9.57
Hybrid	*Era*												
0103-11	2000	100	148	156	134.7	21.9	35.3	42.6	33.3	0.87	0.96	1.06	0.96
0103-15	2000	101	147	157	135.0	22.5	35.9	42.9	33.8	0.89	0.99	1.07	0.98
9801-11	1990	100	145	150	131.6	19.4	30.1	40.3	29.9	0.65	0.75	1.03	0.81
9803-2	1990	98	145	151	131.3	18.8	30.3	40.7	29.9	0.63	0.78	1.04	0.82
8321-21	1980	100	143	152	131.6	16.6	29.9	38.6	28.3	0.51	0.69	1.01	0.74
84218	1980	101	146	151	132.7	17.1	29.9	38.9	28.6	0.50	0.68	1.00	0.76
Mean		100	146	153		19.7	31.9	40.7		0.68	0.81	1.04	
SE		11.4	10.4	9.3	10.4	7.2	6.9	4.7	6.3	0.12	0.11	0.09	0.11
LSD$_{(0.05)}$		3.6	3.3	4.1	3.2	4.5	5.7	5,4	3.2	0.24	0.26	ns	0.12

SE = Standard error.

Mean plant height across all hybrids and both years was 100, 146 and 153 cm under no-N, low-N and optimal-N fertilization respectively. These values indicate 31.5% and 34.6% reduction in plant height under low-N and no-N fertilization respectively. The increase in plant height might be due to increasing level of nitrogen as it increases cell division, cell elongation and nucleus formation. Under low and no-N fertilization, the number of ears plant^{-1} was reduced by 0.13 indicating 16.0%

reduction percentage, while between low-N and optimal-N fertilization 22.1% reduction percentage was recorded. Monneveux et al. (2005) observed that chlorophyll concentration reduction and leaf yellowing are good indicators of N remobilization. Nitrogen deficiency accelerates senescence in the present study by significant decrease in chlorophyll concentration under no-N (51.5%) and low-N fertilization (22.6%) as compared with non-stressed conditions. Leaf N decrease has been reported to have a direct effect on canopy temperature, photosynthesis, resulting in greater kernel abortion and lower grain number (Monneveux et al., 2005).

Grain yield, kernel number and seed weight

Significant differences were detected among the hybrids for grain yield, number of kernels and 1000-seed weight at all N rates (Table 6). Yield parameters increased by decade of hybrid introduction at the three levels of N fertility. Kernel number is a function of photosynthesis at silking and it is closely related with plant growth rate during the critical period for kernel set (Andrade et al., 1999). Across hybrids and years, kernel number doubled at 30 kg N ha^{-1} application and increased by 21.5% at 90 kg N ha^{-1}. N stress probably had an adverse effect mainly on successful fertilization and initiation of kernel formation, and also grain development. A reduction in kernel number was reported to be due to the abortion of ovules after fertilization (Li et al., 2011). Genotypic differences in kernel number in response to low soil N have been linked to differences in N utilization (Jason et al., 2013), which likely reflects the ability to partition biomass and N to the developing ear (D'Andrea et al., 2009) or variation for N assimilate metabolism in the maize cob tissue (Seebauer et al., 2004; Moose and Below, 2009).

There was a linear increase in the weight of 1,000 grains from the oldest to the modern hybrids of 2000 era. The modern hybrids were also more tolerant to N stress compared to the older ones at all N rates. This indicated that the improved hybrids of 2000 era responded better to added N in the savannas. Since the final kernel weight depends largely on grain filling duration, there may be an indication that modern hybrids have a higher ability to either uptake N from the soil or remobilize it from vegetative tissues to grains after silking, delaying leaf senescence, prolonging the filling period and producing heavier grains. This physiological sequence of events has also been reported by Rajcan and Tollenaar (1999), who attributed the higher N efficiency of modern hybrids to a better balanced source: sink ratio. Although kernel weight has increased as a result of selection for grain yield, the increase in the responsiveness of kernel weight to N supply suggests a potential opportunity for exploiting kernel weight as a contributor to future advances in maize grain yield. Therefore, improvement of kernel weight can be explained by increased genetic potential under low-N fertilization (Jason et al., 2013).

Table 6. Grain yield, number of kernels and 1000-seed weight of six maize hybrids of three breeding eras under varying N fertilization at Oke Oyi, Ilorin, Nigeria in 2012 and 2013.

Parameters		Number of kernels				1000-seed weight (g)				Grain yield (t ha^{-1})			
Nitrogen (kg ha^{-1})		0	30	90	Across N	0	30	90	Across N	0	30	90	Across N
Year													
2012		133.4	271.1	340.6	248.4	182.5	215.3	223.6	207.1	1.47	2.88	3.93	2.76
2013		135.6	282.3	342.8	253.6	184.1	220.3	228.8	211.0	1.51	2.90	3.99	2.80
SE		11.36	3.83	4.82	6.67	3.72	7.43	1.56	4.23	7.46	11.82	6.53	8.60
Hybrid	*Era*												
0103-11	2000	140.2	285.3	366.3	263.9	193.4	226.8	232.4	217.5	2.31	3.47	4.67	3.48
0103-15	2000	142.4	291.9	358.7	264.3	192.9	225.9	233.5	217.4	2.24	3.51	4.89	3.55
9801-11	1990	137.4	284.1	348.6	256.7	189.4	217.7	227.3	211.4	1.36	3.32	4.35	3.01
9803-2	1990	130.4	265.4	335.3	243.7	187.4	217.3	225.9	210.2	1.29	3.28	4.32	2.96
8321-21	1980	126.1	232.4	315.8	224.8	167.3	209.5	219.6	198.8	0.67	1.70	2.76	1.71
84218	1980	130.4	251.1	325.6	235.7	169.4	209.7	218.2	199.1	1.09	2.05	2.77	1.97
Mean		134.5	268.4	341.7		183.3	217.8	226.2		1.49	2.89	3.96	
SE		7.3	4.2	3.8	5.1	21.4	8.3	11.8	13.8	0.43	0.48	0.72	0.39
LSD$_{(0.05)}$		14.3	23,7	23,9	38.2	21.6	15,5	14,6	7.4	0.45	0.98	1.45	1.24

SE = Standard error.

Year and N rate were included in the linear mixed model analysis as fixed sources of variance. Although year was not a significant source of variation for grain yield, the main effect of N rate and the interaction effect of year and N rate were highly significant ($p \leq 0.01$; Table 6). Averaged across N rates, grain yields in 2012 and 2013 were 2.76 and 2.80 t ha^{-1} respectively. When averaged across hybrids, grain yield under low-N fertilization was 0.04 t ha^{-1} greater in 2013 compared to 2012. This could be attributed to the increased low-N grain yield of 2013 to slightly high precipitation and cool temperatures, which likely promoted early season N gain and increased net soil N mineralization. The increased N response of 2013 was likely a function of greater residual soil N (i.e., increased grain yield under low-N fertilization) as well as high temperatures at flowering and grain filling, which contributed to decrease in kernel abortion and possibly to increase in duration of grain filling as earlier observed by Jason et al. (2013).

Similarly, there was a differential response of maize hybrids to varying N rates, and N stress significantly reduced grain yield of all the hybrids evaluated in the trials. Generally, newer 2000s hybrids were more tolerant to N stress and had higher grain yield than those ones in the earlier eras at all N rates. Presterl et al.

(2003) conducted studies from 1989 to 1999 across various environments using diverse European maize breeding materials and reported similar magnitude of reduction in grain yield at low N level. Similarly, with the findings of four hybrids representing Brazilian maize germplasm released between the 1960s and 1990s, the most recent hybrids produced higher grain yields at all levels of N (Sangoi et al., 2001). Depending on N treatment, grain yield varied from 0.67 to 4.89 t ha^{-1}. Under low-N fertilization, the range in mean grain yield across the years among hybrids varied from 1.7 to 3.5 t ha^{-1}. Grain yield average across N increased by 48.4% and 62.4 %, as N increased from 0 kg ha^{-1} to 30 kg ha^{-1} and 30 kg ha^{-1} to 90 kg ha^{-1} respectively. When hybrid performance on grain yield is compared in terms of percentage at each N rate across the breeding years, the modern hybrids (0103-15 and 0103-11) were 73.8% and 32.6% more productive than the average of the 1980 decade when 0 kg ha^{-1} and 30 kg ha^{-1} were side-dressed respectively. Genetic gains in grain yield were 42% (between 1980 and 2000 eras) and 36% (between 1990 and 2000 eras) under optimal-N fertilization. These findings are supported by the observation made by Tollenaar et al. (1997), who reported that a newer hybrid (Pioneer 3902, released in 1988) produced approximately 25% higher grain yield than the older hybrid (Pride 5, released in 1959) under both low-N and high-N fertilization. Some researchers revealed that maize grain yield is primarily associated with variations in the number of mature kernels per ear, which in turn depends on crop growth rates at silking (Cañas et al., 2009). Differences in grain yield under high-N fertilization have been attributed to contributions from both N uptake and utilization with varying degrees of importance being assigned to each of these traits by past studies (Presterl et al., 2002; Worku et al., 2007). Compared with earlier released hybrids, Ding et al. (2005) reported that later released hybrids maintained high plant and grain weight under N deficiency because their photosynthetic capacity decreased more slowly after anthesis, associated with smaller non-stomatal limitations due to maintenance of Phosphoenolpyruvate carboxylase (PEPCase) activity, chlorophyll concentration and soluble protein contents.

Correlation of all parameters with yield at each N rate

Grain yield is a function of number of plants per area, the proportion of these plants that produce a harvestable ear, kernel number per ear, and the weight of each individual kernel. Under severed N stress at 0 kg N ha^{-1}, days to anthesis ($r = -0.76$), days to silking ($r = -0.78$), anthesis-silking interval ($r = -0.71$), 1000-seed weight ($r = 0.71$) and number of kernels per ear ($r = 0.80$) were significantly associated with maize grain yield (Table 6). This could be a result of wide differences between the cultivars under these severed N conditions. This study also shows positive correlations between ear leaf chlorophyll, plant height and grain yield. R values are higher but not significant for optimal-N fertilization.

Associations between grain yield and number of grains per ear indicate that the development of initiated spikelets mainly determines yield and closely relates to the assimilate supply to developing grains as earlier reported by Monneveux et al. (2005). Li et al. (2011) also observed similar magnitude of reduction in grain yield under low-N fertilization, and its association with kernels per ear. Association that was observed under low-N conditions between grain yield and anthesis-silking interval, delayed senescence as expressed by either chlorophyll concentration or the number of green leaves above the ear, and ear/tassel weight ratio (data not shown).

Table 7. Correlation of agronomic parameters with grain yield under each nitrogen regime.

Characters	Nitrogen rate (kg ha^{-1})		
	0	30	90
Days to anthesis	-0.76	-0.88	-0.83
P value	0.0713	0.0322	0.0915
Days to silking	-0.78	-0.86	-0.86
P value	0.1211	0.911	0.0012
Anthesis-silking interval (days)	- 0.71	- 0.07	-0.19
P value	0.1113	0.6782	0.6532
Plant height (cm)	0.56	0.43	0.74
P value	0.0211	0.4225	0.1186
Ear leaf chlorophyll (SPAD)	0.46	0.67	0.76
P value	0.2314	0.1356	0.1632
Number of ears plant^{-1}	0.72	0.85	0.83
P value	0.0756	0.2211	0.1213
Number of kernels per ear	0.86	0.79	0.83
P value	0.0111	0.0983	0.1371
1000-seed weight (g)	0.79	0.63	0.64
P value	0.1018	0.0371	0.0975

The strong association between chlorophyll concentration and soluble carbohydrates reported by Rajcan and Tollenaar (1999) confirms this hypothesis and suggests that maintaining N and chlorophyll concentration of leaves during grain filling may lead to maintenance of leaf photosynthesis resulting in better grain filling. Similarly to Lafitte and Edmeades (1994), a significant correlation was noted in the present study between SPAD values (4 weeks after anthesis) and grain yield of hybrids under low-N conditions.

Conclusion

The modern-day hybrids of 2000 breeding era (0103-15 and 0103-11) were more productive than the older hybrids, regardless of the amount of N side-dressed to the soil. Yield improvements in the modern hybrids grown with sufficient N supply were associated with greater plant height, ear leaf chlorophyll content, number of ears plant^{-1}, kernel number, seed weight and grain yield. Decrease in days to anthesis, silking and anthesis-silking interval was also observed. The correlation between grain yield and percent of anthesis-silking interval was only 0.19 and not significant. Genetic gains in grain yield were 42% (between 1980 and 2000 eras) and 36% (between 1990 and 2000 eras) under optimal-N fertilization. The primary enhancement of grain yield under low-N fertilization in modern hybrids has important implications for achieving genetic improvement, yet the ability of the soil to supply N will represent an upper limit to grain yield under low-N fertilization. Therefore, identifying and selectively improving traits associated with fertilizer N response will be necessary to maintain and accelerate the rate of genetic gains needed to increase maize yields.

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GENETSKA POBOLJŠANJA KOD TRI GENERACIJE HIBRIDA KUKURUZA PRI SLABOM I OPTIMALNOM ĐUBRENJU AZOTOM

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Rezime

Komparativno istraživanje reakcije šest hibrida kukuruza: po dva hibrida iz 1980-ih (8321-21 i 8425-8), 1990-ih (9801-11 i 9803-2) i 2000-ih (0103-11 i 0103-15) na suboptimalno i optimalno đubrenje azotom je sprovedeno u mestu Oke-Oyi, Nigerija. Ogledi su postavljeni po planu podeljenih parcela, gde je glavna parcela bila tri doze azota (0, 30 i 90 kg N ha^{-1}), a šest hibrida su bili potparcela. Interakcija hibrida i doze azota imala je značajan uticaj na sve ispitivane osobine, a značajnost se povećavala sa smanjivanjem doze azota. Hibridi kukuruza starijih generacija (iz 1980-ih i 1990-ih) imali su niže prinose zrna za 73,8% u kontrolnoj varijanti đubrenja, za 32,6% pri niskoj dozi azota, dok su pri optimalnoj dozi azota smanjenja bila 34,3% odnosno 15,7% u odnosu na noviju generaciju hibrida iz 2000-ih. U zavisnosti od količine azota, prinos zrna je varirao od 0,67 do 4,89 t ha^{-1}. Broj zrna bio je najmanji usled stresa izazvanog deficitom azota, ali je pokazao pozitivnu i visoko značajnu ($p \leq 0{,}01$) korelaciju sa prinosom zrna pri svim dozama azota. Hibridi najnovije generacije pri optimalnoj dozi azota imali su veći prinos zrna u odnosu na najstariju generaciju za 42% i u odnosu na srednju generaciju hibrida za 9%. Dva moderna hibrida (0103-11 i 0103-15) imala su izrazite prednosti u pogledu svih agronomskih osobina i koncentracije hlorofila u listu pri ispitivanim dozama azota. Poboljšanje osobina povezanih sa reakcijom na azotno đubrivo bi moglo da ubrza genetička poboljšanja prinosa kukuruza.

Ključne reči: cvetanje, prinos zrna, stres usled deficita azota, visina biljke.

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