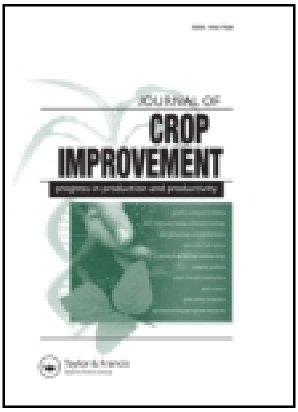

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Genetic Variation for Nitrogen-Use Efficiency Among Selected Tropical Maize Hybrids Differing in Grain Yield Potential

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Low soil nitrogen (N) and sub-optimal N fertilizer applications result in poor grain yield (GY) in maize. Genotypes with improved N-use efficiency (NUE) are particularly beneficial to low-input agriculture. Information on the relative importance of the main components of NUE will facilitate genetic improvement of tropical maize for NUE. This study evaluated genetic variation for NUE among tropical maize hybrids selected for contrasting responses to N. The hybrids were grown in replicated trials from 2006 to 2008 where plots received either no (0 kg N/ha), low (30 kg N/ha), or high (90 kg N/ha) levels of supplemental N. The results documented significant genetic variation for GY and measured NUE component traits among the hybrids, as well as significant interactions between hybrid and N level for all traits except nitrogen harvest index. Under low N, NUE, NUPE, and NUTE increased by 61%, 21%, and 42%, respectively. Grain yield was significantly and positively correlated with NUE, NUPE, and NUTE at both low N and high N. Both NUPE and NUTE were significantly and positively correlated to NUE. Five hybrids (4001/4008, KU1409/4008,

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KU1409/9613, 4008/1808, and 1824/9432) produced similar GY at both low N and high N, but differed in their NUPE and NUTE. Genetic variation was present among the maize hybrids studied for NUE and its components. Although both NUPE and NUTE contributed to high grain yield, the relative importance of the two traits to NUE varied with genotype and level of N.

KEYWORDS genotype, nitrogen, N-utilization efficiency, N-uptake efficiency, low-input agriculture

INTRODUCTION

Maize (*Zea mays* L.) is the most widely cultivated staple food crop in sub-Saharan Africa, providing up to 70% of the daily caloric intake (Martin et al. 2000; Food and Agriculture Organization 2007). In West and Central Africa, not only has maize replaced sorghum and millet as a food staple, it is also a source of cash for smallholder farmers (Smith et al. 1997; Fakorede et al. 2003). The current average maize grain yields (GY) from the major maize-producing ecologies in sub-Saharan Africa are significantly lower than those obtained in most other areas of the world. For example, Pingali and Pandey (2001) reported a yield potential of 5.0 Mg/ha in tropical highlands, 4.5 Mg/ha in tropical lowlands, and 7.0 Mg/ha in subtropical and mid-altitude zones, whereas yields reported in farmers fields in the respective ecologies were 0.6, 0.7, and 2.5 Mg/ha. The current average maize GY across sub-Saharan Africa is only 1.78 Mg/ha (FAO 2009) because of several biotic and abiotic constraints. The soils of the major maize-producing ecologies in Sub-Saharan Africa are inherently low in nitrogen (N), making N deficiency a common feature in maize production (Jones and Wild 1975).

One important cultural practice that accounts for greater than 40% of GY increases in maize is the increased use of supplemental N fertilizer (Smil 2002). However, fertilizer use in Africa is reported to be low, with an average of 8 kg/ha of nutrients (International Fertilizer Development Center 2006; Heisey et al. 2007). The limited local supply of N fertilizers in Africa and inadequate transportation and distribution infrastructure contribute to higher prices compared with global market prices (Mosier et al. 2005). These factors, when combined with the low purchasing power of the predominant resource-poor smallholder farmers in sub-Saharan Africa, perpetuate sub-optimal N fertilizer application on their farms (Bänziger et al. 1999; Crawford et al. 2005).

Breeding for improved N-use efficiency (NUE) can be considered an effective strategy to improve efficiency of maize to utilize available soil N (Presterl et al. 2003). Maize varieties developed through breeding for maximum GY are highly productive and responsive to N application, but they often exhibit relatively low NUE (O'Neill et al. 2004). Consequently, the development and adoption of maize varieties with improved NUE could improve GY with less supplemental N, reduce input costs, and limit the risk of N pollution to the environment (Presterl et al. 2002). The NUE is defined as the GY per unit N available from the soil, including fertilizer N (Moll et al. 1987), and is the product of two major components, namely N-uptake efficiency (NUPE) and N-utilization efficiency (NUTE). The NUPE is the fraction of applied fertilizer N found in the plant at maturity, whereas NUTE is the ratio of GY to plant N. Previous studies have reported the existence of genotypic differences in NUE (Akintoye et al. 1999; Bertin and Gallais 2000; Gallais and Hirel 2004; Worku et al. 2007). Quantitative trait loci (QTL) have also been detected for NUE at various levels of N-fertilizer application (Agrama et al. 1999; Bertin and Gallais 2001). These suggest that many genes and combination of genes are differentially expressed in response to the amount of N provided to the plant (Bertin and Gallais 2000, 2001).

Understanding the major processes associated with NUPE and NUTE is required to design breeding and crop-management strategies to improve overall NUE (Uribelarrea et al. 2007). Prior studies have reported conflicting results regarding the relative importance of these two main components for improving NUE. The NUTE is more important than NUPE under low soil nitrogen in maize (Moll et al. 1982, Ma et al. 1998, Bertin and Gallais 2000) and wheat (Gaju et al. 2011). On the other hand, Kamprath et al. (1982) found that, in maize, NUPE was more important than NUTE. Other studies with tropical (Worku et al. 2007) and temperate (Weisler et al. 2001) maize, as well as wheat (Ortiz-Monasterio et al. 2001), have reported that both NUPE and NUTE were important for optimal performance under low-N conditions. The objectives of this study were therefore to 1) assess genotypic variation in NUPE and NUTE among selected experimental maize hybrids and 2) determine the relative importance of NUPE and NUTE to NUE in maize hybrids.

MATERIALS AND METHODS

Field experiments were carried out at the International Institute of Tropical Agriculture experimental station in Mokwa (9°18′N, 5°04′E, and 457 masl) located in the southern guinea savanna agro-ecology of Nigeria in 2006, 2007, and 2008. The soil type was a lixisol with high sand content (FAO 2003). The field had previously been depleted of nitrogen (N) by planting maize at high densities for two growing seasons without fertilizer application and removing the aboveground biomass after each growing season. The experimental field was cleared, plowed, and harrowed. The physical and chemical properties of the field prior to land preparation in each cropping season, as well as precipitation during the growing season at the location, are shown in Table 1.

TABLE 1 Physical and chemical properties of the soils prior to land preparation in each cropping season and precipitation at the experimental site

	Block								
	0 kg N/ha			30 kg N/ha			90 kg N/ha		
Properties	2007	2008	2009	2007	2008	2009	2007	2008	2009
pH (1:1 H_2O)	4.9	4.8	5.8	5.1	4.9	5.9	5.3	4.7	5.9
Organic carbon (g/kg)	3.8	2.6	4.2	3.7	4.1	5.0	4.0	4.2	5.6
Total N (g/kg)	0.41	0.25	0.42	0.39	0.39	0.54	0.40	0.41	0.60
Available P (mg/kg)	13.35	7.70	5.60	15.66	15.3	6.21	14.75	2.60	6.55
K (cmol/kg)	0.21	0.18	0.23	0.23	0.25	0.18	0.25	0.16	0.17
CEC (mol_c/kg)	3.86	3.77	2.97	4.12	3.15	1.75	4.42	3.42	1.31
Mechanical analyses									
Sand (g/kg)	680	700	740	680	700	820	660	680	820
Silt (g/kg)	150	140	120	140	130	60	160	150	60
Clay (g/kg)	170	160	140	180	170	120	180	170	120
Textural class (USDA)*	SL	SL	SL	SL	SL	LS	SL	SL	LS
Total precipitation (mm) (May to October)									
2006	880								
2007	1222								
2008	1379								

(SL) sandy loam; (LS) loamy sand.

TABLE 2 List of maize hybrids used in this study

S/N	Hybrid	Kernel color	Previous grain yield recorded under low N*
H1	4001/4008	Yellow	High
H2	KU1409/4008	Yellow	High
H3	9450/MOK Pion-Y-S4	Yellow	Low
H4	KU1409/9613	Yellow	High
H5	4008/1808	Yellow	High
H6	4008/9071	Yellow	High
H7	9613/9006	Yellow	Low
H8	4058/Fun. 47-3	White	High
H9	1824/9432	Yellow	High
H10	4058/GH24	White	Low
H11	9071/4058	White	Low
H12	9006/4058	White	Low
H13	OBA SUPER-1 (commercial hybrid)	White	Low
H14	OBA SUPER-2 (commercial hybrid)	Yellow	High

*Source: Meseka (2005).

Twelve single cross maize hybrids, along with two commercial hybrids, were used in the present study. The 12 hybrids were developed at the International Institute of Tropical Agriculture, Ibadan (Table 2), and showed differential grain yields under low-N fertilizer application (Meseka 2005). The two commercial hybrids, Oba Super I and Oba Super II, have been marketed in Nigeria, with the former being N-inefficient and the latter being N-efficient (Sanginga et al. 2003).

The experimental field was divided into three blocks, viz., high N, low N, and no N. The high N block received 90 kg N/ha, the low N block received 30 kg N/ha, and the no N block received 0 kg N/ha. The three blocks were separated from one another by at least 5.0 m to minimize N movement from one treatment to the other. The hybrids were planted in each block in a randomized complete-block design with four replications. The hybrids in each block were planted in four rows of 5.0 m length spaced 0.75 m apart with 0.25 m spacing between plants within a row. Two seeds were hand 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, whereas the outer two rows were used for destructive sampling. At planting, P in the form of single super phosphate and K as muriate of potash were applied at the rate of 60 kg P_2O_5/ha and 30 kg K_2O/ha, respectively. Nitrogen fertilizer in the form of urea was applied in two equal split doses; the first half was applied at 2 weeks after planting (WAP) and the second dose at 4 WAP. Hand weeding at 2 WAP and paraquat (1:1 –dimethyl-4, 4'-bipyridinium dichloride) application at 7 WAP were used to achieve complete weed control.

Nitrogen acquisitions by plants were determined using whole shoots sampled when 50% of the plants in a plot had visible silks and at harvest. At each sampling, four representative plants were cut near the soil surface in each plot. All plant stover at silking and stover (with ears removed) at maturity were chopped and dried in a forced-draft oven at 60°C for 72 hours. The harvested ears were also oven-dried at 60°C for 72 hours. At silking, plant biomass (g/plant) was calculated by dividing the dry weight of each sample by four, whereas total plant biomass (g/plant) at harvest was calculated from the average of the sum of ear and stover weights. Individual samples were ground, passed through a 20-mesh screen, and stored for assay. Grain and stover sub-samples were analyzed for total N concentration (g/kg) using a combustion technique (NA2000 N-Protein, Fisons Instruments, Beverly, MA) at the University of Illinois, Urbana-Champaign. Nitrogen content (g/plant) of stover at silking was calculated by multiplying the N concentration by the dry weight. Total N content (g/plant) at harvest was calculated by multiplying the N concentration for the stover and grain samples by their respective dry weights and summing both values. N-remobilization and post-silking N-accumulation were estimated via the balance method, assuming that all N absorbed after silking was allocated to the grain. Therefore, N-remobilization was calculated as stover N content at silking minus stover N content at harvest. Post-silking N-accumulation, which represents the quantity of total N at harvest absorbed after silking, was calculated as total N content at harvest minus stover N content at silking. Nitrogen harvest index (NHI) was calculated as the ratio of the N content of grains to total N content of aboveground dry matter.

For yield determination, all ears in the inner two rows of each plot were harvested and shelled, and the fresh weight moisture content of shelled grains and number of plants at harvest used to estimate grain yield. Number of plants in the inner two rows per plot was recorded at harvest. Grain yield was expressed in Mg/ha adjusted to 15% moisture content. The GY and plant N content were used to calculate N-use (NUE), N-uptake (NUPE, kg plant N/kg fertilizer N), and N-utilization (NUTE) efficiency.

$$NUE = \frac{GYF - GYU}{NRF} \times 1000 \left(\text{kg grain/kg supplied N}\right) \tag{1}$$

$$NUPE = \frac{NCF - NCU}{NRF} \left(\text{g plant N/g supplied N}\right) \tag{2}$$

$$NUTE = \frac{GYF - GYU}{NCF - NCU} \times 1000 \left(\text{g grain/g plant N}\right) \tag{3}$$

where GYF and GYU represent the grain yield (Mg/ha) in fertilized and unfertilized plots, respectively; NRF is the fertilizer rate (kg/ha); and NCF and NCU represent total plant N yield (kg/ha) in fertilized and unfertilized plots, respectively.

Analysis of variance (ANOVA) was conducted for NUE and related traits using the GLM procedure of SAS (SAS Institute 2003) Analyses were performed across years for each N rate followed by combined analyses for N rates. In both cases, all effects were considered fixed. To assess the association between measured traits at different N input levels, correlation analysis was carried out pairwise between NUE and related traits.

Low N index (LI) was computed from mean grain yield of hybrids using the following procedure of Chantachume et al. (1998):

$$L1 = \frac{X1}{X2} \div \frac{Y1}{Y2},$$

where X1 = mean of GY of hybrid X under low N, X2 = mean of GY of hybrid X under high N, Y1 = mean of GY of all hybrids in low N environment, Y2 = mean of GY of all hybrids in high N environment, and LI > 1 indicates tolerance to low N, whereas LI < 1 is indicative of susceptibility to low N.

RESULTS

Grain Yield

There were significant ($p < 0.01$) differences among hybrids for grain yield at high N and low N levels (Table 3). In the analysis of variance combined across years and N levels, hybrid × N interaction was significant ($p < 0.01$) (Table 4). Mean grain yield, averaged across years, was reduced by 35.2% at low N. Under high N, the hybrid mean grain yields across years varied from 3.3 Mg/ha to 4.4 Mg/ha at high N and from 2.0 Mg/ha to 3.2 Mg/ha at low N. Hybrids 4001/4008 and KU1409/9613 produced the highest yields at high N and low N, respectively, whereas Oba Super-1 was the lowest yielding hybrid under both high N and low N application (Table 5).

The low-N index revealed that eight hybrids had values of 1.0 to 1.3, whereas the remaining six hybrids had values of 0.8 to 0.9 (Table 5). Among the eight hybrids with a 1.0 to 1.3 low-N index, H6 had below-average grain yield under high N, whereas H14 had below-average grain yield at both high N and low N. To visualize the response pattern of hybrids in this study, the grain yields of the hybrids under high N were plotted against their grain yields under low N (Figure 1). Six (H1, H2, H4, H5, H8, and H9) of the eight hybrids with low-N index values (1.0 to 1.3) were found to be efficient and responsive to N application; hybrids H6 was efficient but non-responsive, whereas hybrid H14 was inefficient and non-responsive. Two hybrids (H11 and H12) with low-N index value of 0.8 were responsive to N application, producing grain yields under high N comparable to the N-efficient and N-responsive hybrids. These results suggest that hybrids H11 and H12 have specific adaptation to the high N environment. Overall, hybrids H1 and H4 were the most efficient and responsive hybrids, whereas H13 was the least efficient and responsive hybrid.

N Content and Accumulation

Significant ($p < 0.01$) hybrid and hybrid × nitrogen interactions were observed for aboveground N content both at silking and at harvest. The differences among hybrids for stover N content at silking were more pronounced at high N than at low N (Tables 3 and 4). N content in aboveground dry matter both at silking and at harvest increased with level of N application. At silking, hybrid means for stover N content ranged from 0.97 to 1.26 g/plant under high N and from 0.62 to 0.84 g/plant under low N. At harvest, total N content in aboveground dry matter ranged from 1.50 to 2.00 g/plant under high N and 0.86 to 1.28 g/plant under low N (Table 5). The reduction in total N content at harvest was higher than the corresponding reduction in grain yield at low N. The N-responsive hybrid H2 had the highest total N accumulation after silking and total N content at harvest but remobilized the lowest N from stover to grain under both N rates (Table 5). This indicates that hybrid

TABLE 3 Analysis of variance of the effects of year and hybrid on grain yield (GY, Mg/ha), stover N content at silking (SNCS, g/plant), stover N content at harvest (SNCH, g/plant), grain N content (GNC, g/plant), total N content (TNC, g/plant), and post silking total N accumulation (TNAC, g/plant) of 14 tropical maize hybrids grown under 30 (low N) and 90 (high N) kg N/ha, measured at silking and harvest at Mokwa, Nigeria between 2006 and 2008

Source of variation	DF	Low N						High N					
		GY	SNCS	SNCH	GNC	TNC	TNAC	GY	SNCS	SNCH	GNC	TNC	TNAC
REP	3	62.926***	0.005ns	0.005ns	0.013ns	0.012ns	0.897***	151.021***	0.042ns	0.041*	0.125***	0.114ns	8.685***
Year (Y)	2	0.253ns	5.500***	0.146***	1.038***	1.954***	0.032ns	0.192ns	15.484***	2.082***	4.056***	3.536***	0.277***
Hybrid (H)	13	1.553***	0.051***	0.021***	0.053***	0.119***	0.179***	1.183***	0.083***	0.046***	0.133***	0.207***	0.389***
H*Y	26	0.753***	0.042***	0.010***	0.033***	0.065***	0.084***	1.781***	0.176***	0.082***	0.186***	0.402***	0.196***
Error	123	0.119	0.013	0.005	0.012	0.017	0.023	0.212	0.028	0.014	0.030	0.048	0.049

*, **, ***: significant at 0.05, 0.01, and 0.001 probability levels, respectively; (ns) not significant.

TABLE 4 Analysis of variance for the effects years, N rate, and hybrids on grain yield, N-uptake efficiency (NUPE), N-utilization efficiency (NUTE), N-use efficiency (NUE), nitrogen harvest index (NHI), and N content traits of 14 tropical maize hybrids grown under 30 (low N) and 90 (high N) kg N/ha, measured at silking and harvest at Mokwa, Nigeria, between 2006 and 2008

Source of variation	DF	Grain yield (Mg/ha)	Stover N content at silking (g/plant)	Stover N content at harvest (g/plant)	Grain N content (g/plant)	Total N content at harvest (g/plant)	Post-silking total N accumulation (g/plant)	NUPE at silking	NUPE at harvest	NUTE	NUE	NHI
REP	3	0.375ns	0.019ns	0.019ns	0.100***	0.057ns	0.135*	0.071ns	0.017ns	457.703ns	130.119ns	0.016***
Year (Y)	2	199.531***	19.269***	1.069***	4.539***	5.082***	6.783***	9.410***	2.348***	9556.235***	29088.478***	0.351***
N-level (N)	1	170.897***	12.209***	10.189***	19.570***	57.999***	16.988***	7.096***	2.401***	27041.426***	37251.980***	0.105***
Hybrid (H)	13	2.217***	0.084***	0.046***	0.129***	0.239***	0.371***	0.165***	0.258***	2056.419***	653.840***	0.010***
Y*N	2	14.417***	1.715***	1.159***	0.555***	0.408***	2.799***	0.290***	1.380***	6075.808***	825.362***	0.202***
H*Y	26	1.454***	0.166***	0.046***	0.136***	0.269***	0.120***	0.165***	0.232***	1331.570***	1495.661***	0.007***
H*N	13	0.518***	0.051***	0.021***	0.058***	0.087***	0.197***	0.122***	0.075*	1116.616***	392.544***	0.005ns
H*Y*N	26	1.079***	0.053***	0.047***	0.083***	0.197***	0.160***	0.054***	0.150***	584.124***	648.958***	0.006***
Error	249	0.164	0.02	0.009	0.021	0.033	0.038	0.029	0.04	184.408	94.897	0.003

*, **, *** significant at 0.05, 0.01, and 0.001 probability levels, respectively; (ns) not significant.

TABLE 5 Means of grain yield (GY, Mg/ha), stover N content at silking (SNCS, g/plant), stover N content at harvest (SNCH, g/plant), grain N content (GNC, g/plant), total N content (TNC, g/plant), N remobilization (NR, g/plant), post silking total N accumulation (TNAC, g/plant) and Low-N index of 14 tropical maize hybrids grown under 30 (low-N) and 90 (high-N) kg N/ha fertilizer application at Mokwa, Nigeria, between 2006 and 2008

		Low-N								High-N						
S/N	Hybrids	GY	SNCS	SNCH	GNC	TNC	NR	TNAC	LNI	GY	SNCS	SNCH	GNC	TNC	NR	TNAC
H1	4001/4008	3.09	0.70	0.37	0.69	1.06	0.33	0.36	1.2	4.42	1.05	0.79	1.17	1.95	0.26	0.91
H2	KU 1409/4008	2.93	0.69	0.43	0.85	1.28	0.26	0.59	1.0	4.21	1.01	0.79	1.21	2.00	0.22	0.99
H3	9450/MOK Pion-Y-S4	2.29	0.79	0.34	0.60	0.93	0.45	0.15	0.9	3.68	1.24	0.64	1.20	1.84	0.60	0.60
H4	KU 1409/9613	3.18	0.84	0.33	0.65	0.98	0.51	0.13	1.1	4.30	1.19	0.69	1.21	1.89	0.50	0.71
H5	4008/1808	2.80	0.76	0.38	0.67	1.06	0.38	0.29	1.0	4.18	1.13	0.63	1.15	1.78	0.50	0.65
H6	4008/9071	2.75	0.67	0.39	0.59	0.98	0.28	0.31	1.3	3.70	1.26	0.62	0.88	1.50	0.64	0.24
H7	9613/9006	2.46	0.67	0.30	0.64	0.95	0.37	0.26	0.9	3.90	1.04	0.67	1.26	1.93	0.37	0.89
H8	4058/Fun 47-4	2.73	0.72	0.36	0.70	1.06	0.36	0.34	1.0	4.25	1.12	0.72	1.25	1.97	0.40	0.85
H9	1824/9432	2.95	0.78	0.28	0.58	0.86	0.50	0.08	1.1	4.24	0.97	0.58	1.12	1.70	0.39	0.73
H10	4058/GH 24	2.33	0.63	0.29	0.61	0.89	0.34	0.27	0.9	3.83	1.05	0.72	1.11	1.83	0.34	0.78
H11	9071/4058	2.23	0.76	0.33	0.66	0.99	0.43	0.23	0.8	4.28	1.11	0.66	1.22	1.87	0.45	0.77
H12	9006/4058	2.27	0.77	0.32	0.70	1.02	0.45	0.25	0.8	4.27	1.07	0.72	1.16	1.88	0.36	0.80
H13	OBA SUPER-1	2.02	0.67	0.33	0.65	0.98	0.34	0.31	0.9	3.34	1.08	0.69	1.03	1.72	0.39	0.64
H14	OBA SUPER-2	2.47	0.62	0.34	0.62	0.96	0.28	0.34	1.0	3.90	1.08	0.75	1.01	1.76	0.33	0.68
Mean		2.61	0.72	0.34	0.66	1.00	0.38	0.28		4.03	1.10	0.69	1.14	1.83	0.41	0.73
CV (%)		13.2	16.0	20.2	16.4	12.9	32.0	54.1		11.4	15.1	16.9	15.3	12.0	39.6	30.4
LSD (0.05)		0.28	0.09	0.06	0.09	0.10	0.10	0.17		0.37	0.13	0.09	0.14	0.18	0.13	0.26

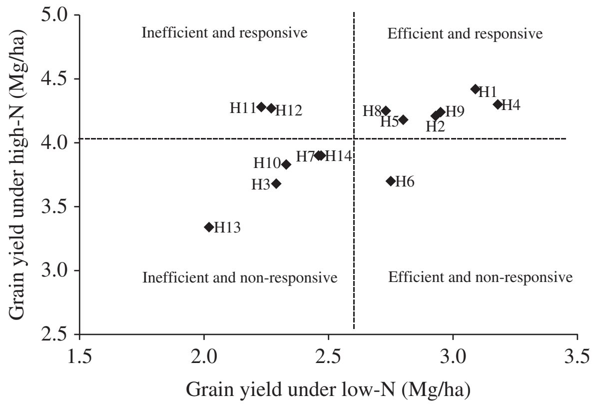

FIGURE 1 Biplot for grain yields of 14 tropical maize hybrids at high and low levels of applied nitrogen fertilizer. Broken lines represent mean grain yields of all hybrids.

H2 possessed a high efficiency for N absorption during grain filling. On the other hand, the N-responsive hybrid H4 accumulated the lowest stover N after silking, but remobilized the highest N from stover to grain under low N. The range in grain N content was 0.88 to 1.26 g/plant under high N and from 0.58 to 0.85 g/plant under low N. Hybrid H2 had significantly higher grain N content at low N than those of other hybrids. Although the N-non-responsive hybrid H7 had the highest grain N content at high N, the value was not significantly different from that of H2 (Table 5). On average, 72% of the total N content at harvest was accumulated at silking at low N, whereas 60% of the total N content at harvest was accumulated at silking under high N. The stover N remobilized to meet kernel demand was 52.8% at low N and 37.3% at high N.

Efficiencies of N-Uptake, N-Utilization, and N-Use, and Nitrogen Harvest Index

Hybrid effects were significant ($p < 0.01$) for NUE, NUPE, and NUTE at both high N and low N. Significant ($p < 0.01$) differences in nitrogen harvest index (NHI) were observed among hybrids only under high N (Table 6). Hybrid × N interactions were significant ($p < 0.01$) for NUE, NUPE, and NUTE but not for NHI (Table 4). The NUPE at silking and at harvest were lower at high N than at low N. The NUPE was reduced by 60% at silking and by 21% at harvest at high N. The NUTE and NUE were also reduced by 42% and by 61% at high N, respectively. The NHI was reduced by 6.5% at high N, suggesting a relative stability of this trait across N levels (Table 7).

The range in NUPE for hybrids at silking was 0.6 to 1.0 at low N and from 0.4 to 0.6 at high N. The NUPE at harvest varied from 0.7 to 1.2 at low N and from 0.6 to 0.9 at high N. The NUTE varied from 39.8 to 95.7 at low

TABLE 6 Analysis of variance on the effects of year and hybrid on N-uptake efficiency at silking (NUPE1), N-uptake efficiency at harvest (NUPE2), N-utilization efficiency (NUTE), N-use efficiency (NUE), and nitrogen harvest index of 14 tropical maize hybrids grown under 30 (low N) and 90 (high N) kg N/ha, measured at silking and harvest at Mokwa, Nigeria, between 2006 and 2008

		Low N					High N				
Source of variation	DF	NUPE1	NUPE2	NUTE	NUE	NHI	NUPE	NUPE	NUTE	NUE	NHI
REP	3	0.057ns	0.067ns	917.028*	142.180ns	0.004ns	0.030*	0.029ns	99.025ns	30.640ns	0.017***
Year (Y)	2	6.138***	3.483***	413.438ns	19049.809***	0.013*	3.561***	0.245***	15218.604***	10864.032***	0.540***
Hybrid (H)	13	0.267***	0.242***	2914.790***	935.197***	0.006ns	0.020*	0.090***	258.245***	111.187***	0.008***
H*Y	26	0.163***	0.242***	1504.230***	1795.499***	0.004ns	0.056***	0.141***	411.464***	349.120***	0.01***
Error	123	0.047	0.063	292.900	164.226	0.004	0.011	0.017	66.795	26.841	0.003

*, **, *** significant at 0.05, 0.01, and 0.001 probability levels, respectively; (ns) not significant.

TABLE 7 Effects of nitrogen fertilizer application on N-uptake efficiency, N-utilization efficiency, and N-use efficiency and nitrogen harvest index of 14 maize hybrids grown under 30 (low N) and 90 (high N) kg N/ha, measured at silking and harvest at Mokwa, Nigeria, between 2006 and 2008

	N-level					
	Low N		High N			
Traits	mean	se	mean	se	LSD (0.05)	% reduction
At silking						
N-uptake efficiency	0.77	0.03	0.48	0.02	0.04	−60.4
At harvest						
Nitrogen harvest index	0.66	0.00	0.62	0.01	0.01	−6.5
N-uptake efficiency	0.99	0.03	0.82	0.02	0.04	−20.7
N-utilization efficiency	60.55	2.04	42.61	1.37	2.92	−42.1
N-use efficiency	55.36	2.05	34.30	1.13	2.09	−61.4

N and from 35.0 to 51.7 at high N. The NUE ranged from 43.3 to 73.3 at low N and from 29.8 to 38.3 at high N (Table 8). At silking, the six N-responsive hybrids (H1, H2, H4, H5, H8, and H9) had medium to high NUPE under low N. Three of these hybrids (H1, H4, and H9) had below-average NUPE at harvest (Figures 2 and 3). The N-non-responsive hybrid, H3, had a high NUPE at silking and harvest, but a low NUTE under both low N and high N. Among the N-responsive hybrids, H1, H4, and H9 had high NUTE under both low N and high N, whereas the remaining three hybrids had below-average NUTE under low N (Figure 4). Although five of the high-yielding hybrids under low N (H1, H2, H4, H5, and H9) did not differ significantly in grain yield under both high N and low N, they differed significantly in NUPE and NUTE under low N. Hybrids H2 and H5 had high NUPE, whereas hybrids H1, H4, and H9 exhibited high NUTE. The results showed that NUPE and NUTE contributed to high grain yield under both high N and low N, and hybrids could differ in the physiological mechanisms by which they achieve NUE.

Relationships Among Measured Traits

The correlations among measured traits are presented in Table 9. The relationship between grain yield and N content at silking was positive at both high N and low N. At harvest, the correlation between grain yield and stover N content was positive at low N but was negative at high N. The correlations of grain yield with total N content at harvest, and grain N content were positive at both low N and high N. Grain yield was positively correlated with NUPE and NUTE both at silking and at harvest. However, the correlation coefficient between grain yield and NUTE at high N was more than twice

TABLE 8 Means of N-use efficiency, N-uptake efficiency, N-utilization efficiency, and Nitrogen harvest index of 14 tropical maize hybrids grown under 30 (low-N) and 90 (high-N) kg N/ha fertilizer application at Mokwa, Nigeria, between 2006 and 2008

		N-use efficiency		N-uptake efficiency at silking		N-uptake efficiency at maturity		N-utilization efficiency		Nitrogen harvest index	
S/N	Hybrids	Low N	High N	Low N	High N	Low N	High N	Low N	High N	Low N	High N
H1	4001/4008	59.86	34.76	0.83	0.48	0.93	0.84	67.51	44.34	0.64	0.59
H2	KU 1409/4008	46.53	29.78	0.78	0.45	1.16	0.81	44.66	37.31	0.66	0.61
H3	9450/MOK Pion-Y-S4	60.33	35.53	0.94	0.59	1.07	0.89	53.90	35.22	0.64	0.63
H4	KU 1409/9613	73.31	36.85	1.03	0.53	0.90	0.81	81.07	45.97	0.66	0.63
H5	4008/1808	56.92	34.26	0.83	0.50	1.01	0.77	58.21	48.95	0.64	0.65
H6	4008/9071	58.47	29.98	0.48	0.51	0.84	0.60	71.70	51.70	0.60	0.58
H7	9613/9006	56.45	34.75	0.67	0.44	0.90	0.88	69.63	40.25	0.67	0.66
H8	4058/Fun 47-4	56.37	35.61	0.77	0.49	1.16	0.93	49.64	38.63	0.66	0.63
H9	1824/9432	68.76	37.23	0.92	0.42	0.72	0.74	95.66	47.27	0.67	0.65
H10	4058/GH 24	54.85	34.91	0.68	0.48	0.91	0.86	62.48	39.92	0.68	0.61
H11	9071/4058	46.56	38.34	0.77	0.46	1.08	0.88	42.69	43.75	0.67	0.64
H12	9006/4058	46.91	37.81	0.87	0.47	1.22	0.92	39.79	40.80	0.68	0.60
H13	OBA SUPER-1	46.43	30.12	0.63	0.46	1.05	0.79	52.24	41.86	0.66	0.61
H14	OBA SUPER-2	43.31	30.29	0.60	0.47	0.88	0.77	58.50	40.51	0.65	0.58
Mean		55.36	34.30	0.77	0.48	0.99	0.82	60.55	42.61	0.66	0.62
CV (%)		23.15	15.10	28.01	21.57	25.35	15.90	28.27	19.18	9.28	8.29
LSD (0.05)		10.36	4.19	0.17	0.08	0.20	0.11	13.83	6.60	0.05	0.04

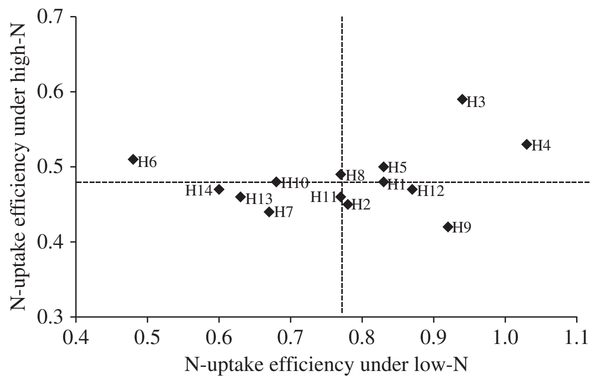

FIGURE 2 Biplot of N-uptake efficiencies at silking in 14 tropical maize hybrids at high and low levels of applied nitrogen fertilizer. Broken lines represent mean N-uptake efficiencies of all hybrids.

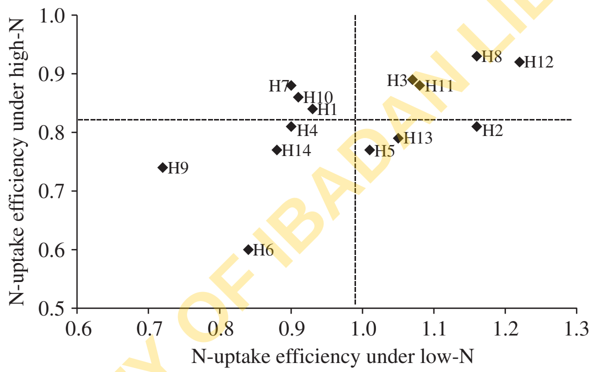

FIGURE 3 Biplot of N-uptake efficiencies at harvest in 14 tropical maize hybrids at high and low levels of applied nitrogen fertilizer. Broken lines represent mean N-uptake efficiencies of all hybrids.

its corresponding values at low N. The NUTE also had significant correlation with the number of kernels at high N than at low N (data not shown).

The NUPE, measured at silking, had strong positive correlations with stover N content at silking at both high N and low N. Stover N content at silking showed positive and significant ($p < 0.01$) association with NUE and its components, with stronger correlation coefficients at high N relative to low N. Grain N content was significantly ($p < 0.01$) and positively correlated with NUPE, NUE, and NHI both at silking and harvest. The relationship of grain N content with NUTE was negative at low N but positive at high N. The NUE had significant ($p < 0.01$) positive correlations with NUTE and NUPE at both levels of N, with a stronger association at high N than at low N. The NHI was positively and significantly ($p < 0.01$) correlated with NUE and NUTE at high N but not at low N. The NUPE at silking was correlated

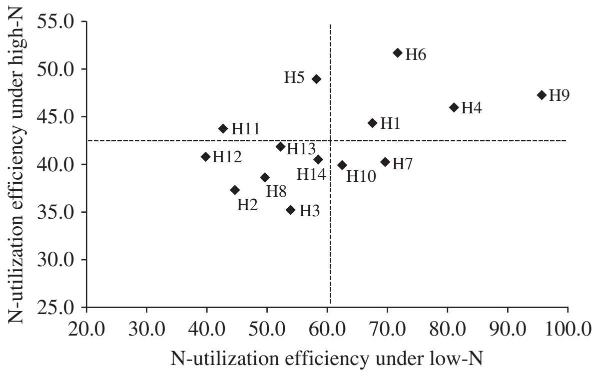

FIGURE 4 Biplot for N-utilization efficiencies in 14 tropical maize hybrids at high and low levels of applied nitrogen fertilizer. Broken lines represent mean N-utilization efficiencies of all hybrids.

($p < 0.01$) to NUTE only at high N. The NUPE at harvest and NUTE were negatively correlated at both levels of N, with the correlation coefficient at low N being more than twice that at high N.

DISCUSSION

In the present study, the observed 35% reduction in grain yield under low N is comparable with the results of Bänziger et al. (1999) and Bertin and Gallais (2000), who reported 40% and 38% reduction in maize GY under low N, respectively. The 14 hybrids included in this study exhibited significant differences in grain yield, and NUE and NUE-related traits. Hybrid × N rate interaction was significant for GY and NUE-related traits, indicating that the hybrids differed in their response pattern to N, contrary to the results reported in other studies (Kling et al. 1997; Oikeh et al. 1998; Akintoye et al. 1999). Our findings agree with the results of Agrama et al. (1999) and Worku et al. (2007) for tropical maize, Bertin and Gallais (2000) for European maize, and O'Neill et al. (2004) for temperate maize. The significant hybrid × N rate interaction obtained in the present study could result from the inclusion of hybrids selected for different responses to low N application. The differences in GY among hybrids under a particular level of N-fertilizer application could be attributed to differences among the maize hybrids for NUPE and NUTE (Beauchamp et al. 1976; Pollmer et al. 1979).

The NUE and its two primary component traits decreased from low N to high N, with significant hybrid differences at both low N and high N, consistent with results from previous studies (Akintoye et al. 1999; Bertin and Gallais 2000; Uribelarrea et al. 2007; de Souza et al. 2008). Uribelarrea et al. (2007) evaluated maize hybrids at six N rates and reported that NUE,

TABLE 9 Correlation coefficients among measured traits of 14 tropical maize hybrids grown under 30 (low-N) and 90 (high-N) kg N/ha fertilizer application at Mokwa, Nigeria, between 2006 and 2008 (low N above and high N below the diagonal)

	Stover N content at silking (g/plant)	Grain N content (g/plant)	Total N content at harvest (g/plant)	N-uptake efficiency at silking	N-uptake efficiency at harvest	N-utilization efficiency	N-use efficiency	Nitrogen harvest index	Grain yield (Mg ha^{-1})
Stover N content at silking (g/plant)		0.61**	0.62**	0.89**	0.31**	0.15*	0.50**	0.18*	0.77**
Grain N content (g/plant)	0.69**		0.94**	0.52**	0.63**	−0.28**	0.30**	0.49**	0.60**
Total N content at harvest (g/plant)	0.49**	0.82**		0.52**	0.64**	−0.29**	0.29**	0.17*	0.63**
N-uptake efficiency at silking	0.97**	0.67**	0.45**		0.44**	0.12ns	0.57**	0.21**	0.68**
N-uptake efficiency at harvest	0.41**	0.75**	0.87**	0.43**		−0.45**	0.45**	0.20**	0.41**
N-utilization efficiency	0.40**	0.15*	−0.23**	0.44**	−0.17*		0.51**	−0.04ns	0.33**
N-use efficiency	0.61**	0.59**	0.28**	0.67**	0.42**	0.79**		0.12ns	0.76**
Nitrogen harvest index	0.52**	0.66**	0.12ns	0.55**	0.17*	0.56**	0.63**		0.14ns
Grain yield (Mg/ha)	0.77**	0.68**	0.38**	0.77**	0.36**	0.72**	0.90**	0.67**	

*, ** significant at 0.05 and 0.01 probability levels, respectively; (ns) not significant.

NUPE, and NUTE were negatively related to N availability. Akintoye et al. (1999) reported a mean NUE of 55 kg/kg at low N, 32 kg/kg at medium N, and 25 kg/kg at high N. Similarly, mean NUE in the current study was 55.4 kg/kg at low N and 34.3 kg/kg at high N. Mean NUTE obtained at low N and at high N in the present study were similar to those reported by Worku et al. (2007) and de Souza et al. (2008) for tropical maize, and Coque and Gallais (2007) for European maize.

The NUE has been defined as the ability of a genotype to realize an above-average GY under conditions of low N availability (Graham 1984; Sattelmacher et al. 1994). In the present study, hybrids H1, H2, H4, H5, and HE9 produced similar above-average GY under both high N and low N application but differed in their NUPE and NUTE. These hybrids may thus possess either a strong capacity for N-uptake and storage or high N remobilization from vegetative tissues to kernels or a combination of these processes (Stromberger et al. 1994). Hybrids H2 and H5 exhibited high NUPE, whereas hybrids H1, H4, and H9 exhibited high NUTE to achieve high GY. It appears that each set of hybrids employed either NUPE or NUTE for achieving high GY under limiting N supply. These results were contrary to those of Moll et al. (1982) and Bertin and Gallais (2000) in maize, as well as Gaju et al. (2011) in wheat, who reported that NUTE is more important than NUPE under low N conditions. The results were also contrary to the findings of Kamprath et al. (1982), who reported that NUPE was more important than NUTE under low-N conditions. However, the results of the present study were consistent with those of Worku et al. (2007) and Weisler et al. (2001) for maize, and Ortiz-Monasterio et al. (2001) for wheat, who reported that both NUPE and NUTE were important for optimal performance under limiting soil N. The hybrids H11 and H12, which showed susceptibility to N stress under low N, had comparable yields with hybrids H1, H2, H4, H5, and H9 under high N, indicating that the two hybrids were inefficient but responsive to N and therefore required a high N input to attain their yield potential (Sangoi et al. 2001).

The positive and significant correlations between the components of NUE and GY were similar to the results reported by Heuberger (1998) and Kamara et al. (2003). Although the relationship between GY and NUPE at silking under high N was similar to that observed under low N, the stronger correlations of GY with NUPE at harvest under low N suggested that NUPE could play a relatively more important role in determining GY under low N supply (Kamprath et al. 1982; Presterl et al. 2002). The negative correlation between NUTE and total N content under high N and low N showed that maize hybrids absorbing high quantities of N might not necessarily utilize the absorbed N efficiently. The observed negative and significant correlations between NUPE and NUTE at both low N and high N also suggested that simultaneous improvement in both traits might not be possible.

In conclusion, genetic variation for NUE and its components was present among the tropical maize hybrids studied. Both NUPE and NUTE contributed to high GY under low N and high N. Although the relative importance of NUPE and NUTE to NUE varied with hybrid and environment, simultaneous improvement of the two traits would appear to be difficult.

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