

Physiological and morphological changes associated with recurrent selection for low nitrogen tolerance in maize

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Abstract Increase in maize grain yield in West Africa can be achieved by developing maize varieties tolerant to low soil nitrogen (N) and improving soil fertility. Six maize populations were evaluated in two locations in Nigeria under low-N (45 kg N ha⁻¹) and high-N (90 kg N ha⁻¹) conditions to identify morphological and physiological traits that changed in genotypes that had undergone recurrent selection for tolerance to low soil N and to determine the relationship between physiological and yield traits in both nitrogen environments. Results revealed that improved cycles of three populations displayed longer leaf area duration, larger leaf area ratio, larger leaf area index and higher crop growth rate (CGR) at silking than their earlier versions at 45 and 90 kg N ha⁻¹. Net assimilation rate increased significantly in response to selection in three out of six populations at 45 kg N ha⁻¹. Significant yield changes were observed in response to selection in three populations at 45 kg N ha⁻¹ and four populations at 90 kg N ha⁻¹, accompanied by increments in 100 kernel weight in three populations and number of kernels per row in one population. Grain yield and 100 kernel weight reduced by 31 and 5% respectively

in response to N-stress. Among physiological traits, only CGR and SPAD chlorophyll readings had significant positive relationship with grain yield under low and high N conditions. Hence, CGR and SPAD chlorophyll values can be utilized in selecting for tolerance to low-N in maize for West Africa region.

Keywords Grain yield · Physiological traits · Recurrent selection · Nitrogen · Maize

Introduction

Low soil nitrogen is a major limiting factor to maize productivity in West and Central Africa with annual losses in yield varying from 10 to 50% (Wolfe et al. 1988). Low soil nitrogen in the sub-region is a result of leaching of soil nitrogen below the root zone due to torrential rainfall, poor weed control, (Lafitte and Edmeades 1994) removal of crop residue for animal feed and also the application of sub-optimal levels of fertilizers due to high costs. These interlinked factors necessitate the development of N-efficient cultivars that take up N and/or utilize N efficiently. Knowledge of the physiology and genetics of N-uptake and utilization is crucial to the development of N-efficient cultivars.

Recurrent selection methods have been widely used by maize breeders to improve maize for tolerance to low soil nitrogen (Ajala et al. 2012). Genetic gains

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have also been reported in physiological traits that promote efficiency in growth, development and partitioning in the maize plant (Duvick 2005). Changes in light interception due to increased leaf area index (LAI) and in light utilization, maintenance of green leaf area and leaf photosynthesis during grain-filling period resulted in increase in dry matter and grain yield of maize (Lee and Tollenaar 2007). LAI, crop growth rate (CGR) and net assimilation rate (NAR) are crucial factors in the measurement of photosynthesis (Aliu et al. 2010).

However, there are contradicting research results on the growth analysis parameters that significantly affect grain yield. Kumar and Singh (2001) argued that LAI and leaf area duration (LAD) are important components for determining the dry matter accumulation and grain yield in maize while Adebo and Olaoye (2010) reported that LAI and LAD were not determinants of grain yield in the crop. However, Fakorede and Mock (1978) reported on significant changes in morphological and physiological characteristics associated with recurrent selection for grain yield in BSSS(R)C7 × BSCBI(R)C7 compared to BSSS(R)C0 × BSCBI(R)C0 maize hybrids. Gains from selection have been reported in the low soil nitrogen tolerant population developed in West and Central Africa and used in this study (Ajala et al. 2012) but little information is available on the physiological traits that may have changed and resulted in the observed increase in grain yield. The study was therefore carried out to identify the morphological and physiological traits that enabled yield changes in populations that had undergone two to three cycles of selection for tolerance to low nitrogen and determine the relationship between physiological traits and yield of maize.

Materials and methods

Experimental location

The experiments were conducted at experimental stations of the International Institute of Tropical Agriculture (IITA) in Ikenne (6°87'N, 3°7'E) and Ibadan (7°30'N, 3°54'E), Nigeria in 2012, 2013 and 2014. The soil in the experimental station at Ikenne is entric nitosol (FAO/UNESCO 1974), while the soil in Ibadan is typically ferric luvisols. Samples of soils in

both locations were collected and routine analysis conducted before experimentation.

Genetic materials used in the study

The materials used were obtained from the International Institute of Tropical Agriculture (IITA) Ibadan, Nigeria. Six maize populations namely: LNTP-Y, LNTP-W, TZPB Prolific, TZL Comp 1-W, BR 9928 DMRSR, and Acr 97 TZL Comp 1-W, were used in the study. The development of LNTP-Y, LNTP-W and TZPB-SR prolific are was earlier reported in Ajala et al. (2012). Specifically, a total of 194 selected families comprising of 34 selected from Pop.28-SR X KU 1414-SR/SR, 84 from Pop.28 SR X TZPB-SR LN C0 and 78 from TZPB-SR Prol.C1 X KU1414-SR/SR were inter-crossed in 1996 to develop a broad-based low-N tolerant (LNTP) population. By 1998, two cycles of full-sib selections under low N had been completed in the population. However, as this population had mixed grain colour, selection for yellow grained colour was done from 1998 to 1999 under low N stress ($\leq 30 \text{ kg N ha}^{-1}$) at two sites, Mokwa (9°18'N, 5°4'E) and Zaria (11°11'N, 7°38'E), in Nigeria. This resulted in the selection of 30 full-sib families to eventually form LNTP-YC3 (Ajala et al. 2012). White seeds from seven selected families and two additional selections from 1998 trial were crossed to LNTP-W to form LNTP-W × LNTP C0 and renamed LNTP-WC3 after the two varieties were release in Nigeria in 2009 (NACGRAB 2014). LNTP-W itself was developed by the IITA station in Cote d'Ivoire from germplasm selected at CIMMYT Mexico for tolerance to low-N.

TZPB-SR Prolific was developed from TZPB maize population by screening 250 S1 families in 1990 for grain yield and ears/plant at Ibadan, Nigeria and selecting 102 families for further screening resulting in the selection of 19 best prolific families for recombination to form TZPB Prolific and further improved to generate the cycle three (C3) using full-sib family selection. TZPB was developed at IITA in the early 1970s and released in 1975 (NACGRAB 2014).

TZL COMP1-W, Acr TZL Comp1-W and BR 9928 DMRSR were also released in Nigeria in 2001, 2008 and 2009 respectively (NACGRAB 2014). TZL COMP1-W was developed at IITA in 1988 by crossing a Maize streak virus-resistant population; TZB-SR

with seven *Striga*-resistant inbred lines (Tzi 1, Tzi 9, Tzi 12, Tzi 13, Tzi 17, Tzi 24 and Tzi 30) identified from registered IITA inbred lines (Kim et al. 1987). Thereafter, the population was improved using S/S2 line or full-sib family selection schemes under artificial infestation with *Striga hermonthica* (L. Benth) at Abuja (9°16N, 7°20E) and Mokwa (9°18 N, 5°4E) in Nigeria (Menkir and Kling 2007) till the sixth cycle (TZL COMP1-W C6) of improvement. ACR 97 TZL COMP1-W was subsequently developed by intercrossing the top 14 full-sib families from the fifth cycle (C5) of selection in TZL COMP1 (Menkir and Kling 2007). BR 9928 DMRSR was developed from Pop 28, a tropical late maturing yellow variety developed from a mixture of Caribbean, Mexican and Central America and Brazilian germplasm by CIMMYT and converted for streak, downy mildew (Ajala et al. 2003) and stem borer resistance at IITA. Eventually, full-sib families from the three populations were evaluated under low N stress ($\leq 30 \text{ kg N ha}^{-1}$) and best top 10% performing progenies recombined to form their low-N (LN) versions.

Selection procedure

Full-sib family selection was used to improve on levels of tolerance to low soil nitrogen in each of the populations. For each cycle of improvement, a minimum of 250 full-sib families were usually generated in each population at Ibadan during the off season and under irrigation by planting each selected family from the previous cycle next to a balanced bulk of all the selected families from the population to be improved in the next row and pairing individual plants from the two rows. At the same time, the selected families were recombined to form the new and improved version of the population. Using this method, a cycle of improvement was completed in two seasons. The generated families were then evaluated under 30, and 90 kg N ha^{-1} at two low N sites, Mokwa (longitude 5°40'E and latitude 9°18'N), and Zaria (longitude 07°38'E and latitude 11°11'N) in Nigeria. A 10% selection intensity was applied to identify the best families for recombination by using rank summation index (Mulumba and Mock 1978) involving ears/plant, anthesis-silking interval (ASI), ear aspect, stay-green quality, and grain yield under low N (30 kg N ha^{-1}) together with grain yield under high N (90 kg N ha^{-1}). Ear aspect was obtained as a visual

score of 1–9, where 1 = clean, uniform, large and well filled ears and 9 = rotten, variable, small and partially filled ears while stay green was rated as proportion of dead leaves below the ear with 0 = all leaves below the ear not dead and 10 = all (100%) leaves below the ear dead.

Experimental design and procedures

Experiment were conducted in six environments namely, two low-N (45 kg N ha^{-1}) and four high-N (90 kg N ha^{-1}) from two, Ibadan and Ikenne locations in Nigeria. Trials at Ikenne were planted on August 28, 2012 during the late planting season in each of two N environments represented by one low-N level (45 kg N ha^{-1}) and one high N level (90 kg N ha^{-1}). Trials in Ibadan were planted on April 17, 2013 in two N environments during the early planting season, and on 19 April 2014 in one low-N and one high-N environment. Trials in each N-block were laid out as randomized complete block (RCBD) with four replications. The N-fertilizer levels were separated from one another by at least 10.0 m. In each block (for each N level), plots consisted of two rows of 5.0 m length. Inter-row and intra-row spacing were 0.75 and 0.25 m, respectively. Two seeds were planted per hill and later thinned to one to obtain a plant population density of 53,333 plants per hectare. The plots were separated by a common border variety which was earlier maturing to allow for data collection from the two test rows. One row was used for yield determination, plant height and leaf chlorophyll measurements while the other row was used for destructive sampling. Both low and high-N blocks received 45 kg N ha^{-1} from NPK 15:15:15 application at 2 weeks after sowing (WAS), the high N blocks received additional 45 kg N ha^{-1} from application of Urea at 6 weeks after sowing. Urea was inadvertently applied on a low N field planted in Ibadan during the early season of 2013 resulting in the conversion of the field to a high-N trial. Weeds were controlled by a pre-planting spray of Round-Up (*N*-phosphonomethyl glycine) at 3 weeks before planting. A mixture of metalachlor plus atrazine and paraquat was applied at planting at the rate of 1.6 and $1.0 \text{ kg a.i. ha}^{-1}$ for pre-and post-emergence weed control and was supplemented with hand weeding as required after planting.

Data collection and analysis

Data were collected in each trial from the two test rows but eliminating the border plants at the beginning and the end of each row. Days from sowing to 50% pollen-shed (anthesis date) and 50% silk extrusion (silking date) were recorded and anthesis silking interval (ASI) was then obtained as the difference between the number of days to silking and days to anthesis. Plant height was estimated as the distance from the ground level to the flag leaf from ten tagged plants per plot.

Leaf chlorophyll concentration was measured at silking in the middle of the upper ear leaf (Chapman and Barreto 1997) on ten competitive per plot just before destructive sampling using a portable single-photon Avalanche Diode (SPAD) chlorophyll metre. Leaf area was measured from five randomly selected plants per plot using the leaf area metre (LICOR 3100). Ten plants were harvested at silking (t1) and another ten at grain filling (t2) representing R1 and R3 stages of maize growth respectively (Hanway 1971). Harvested plants were separated in the laboratory into leaves, stem, roots, panicles and ears. Dry weights were determined after plant parts were dried for 72 h at 75 °C in a force drought oven to constant weight and together with leaf area measurements used to estimate, LAI, LAD, LAR, CGR, NAR were computed on the basis of the formulae used by Beadle (1987).

At maturity, cob length (cm), number of kernels per row, 100 kernel weight and number of kernel rows were determined as an average from five randomly selected cobs harvested per plot. Ears per plant was estimated at the total number of ears harvested per plot divided by the number of plants harvested per plot, while grain yield was measured in mg/ha as grain weight per plot adjusted to 15% moisture content.

Analysis of variance (ANOVA) for a randomized complete block was carried out on agronomic and physiological traits using the GLM procedure from SAS statistical software (SAS Institute Inc. 2013). Trials in each year, season and location were considered random and combined to form either low- or high-N environments. Correlation coefficients were further determined between low and high-N parameters at in both locations. *b*-values from linear regressions of traits from population that had completed more than two cycles of selection were used to estimate gains from selection comparable to the linear contrast of (Bolaños and Edmeades 1993) while

conventional orthogonal comparison was used for the remaining three populations that had undergone only one cycle of selection for tolerance to low-N.

Results

Pre-planting soil chemical properties and particle size distribution of experimental sites

Result of soil analysis revealed that soils in both experimental sites had sand–silt–clay composition to be described as loamy sand. The pH of soils ranged from 6.0 to 6.5, implying that soils were slightly acidic. Total nitrogen of soils ranged from 0.08 to 0.12 g kg⁻¹ thus indicative of the need to apply nitrogenous fertilizer for enhanced crop growth and yield. The soils had a low concentration of exchangeable bases (Table 1).

Effects of recurrent selection and nitrogen levels on physiological traits of maize

Variances attributable to environment and genotype were significant for all physiological traits except for LAI under high-N condition (Table 2). Environment × genotype interaction was highly significant for all physiological traits, however, genotype × low-N interaction was not significant for crop growth rate.

Results obtained under low-N revealed significant increases in LAI values for the cycles of selection in three out of the six populations. LAI increments of 0.73, 0.31 and 0.35 were observed in BR9928 DMSR, LNTP-Y and TZPB Prol. populations respectively (Table 3). Improved versions of Acr97 TZL Comp1-W, TZPB prol and TZL Comp1-W had significantly higher LAD values than their earlier versions. Similarly, significant increases in LAR were observed in BR9928 DMSR, LNTP-W and TZL Comp1-W due to selection. Furthermore, selection significant increased CGR values by 3.95, 2.22 and 4.00 g m⁻² day⁻¹ in Acr97 TZL Comp1-W, LNTP-W and TZL Comp1-W populations, respectively (Table 3).

Under high-N (90 kg N ha⁻¹) environment, significant LAI increments in response to selection were observed in improved versions of BR9928 DMSR, LNTP-Y and TZPB populations (Table 3). Higher LAD values were observed in improved versions of Acr 97 TZL Comp1-W, TZPB Prol. and TZL Comp1-

W populations relative to their earlier versions. Increases in CGR values were also obtained in response to selection in Acr97 TZL Compl1-W, BR9928 DMSR and TZL Compl1-W populations.

Shorter ASI values of were obtained in response to selection in BR9928 DMSR (and LNTP-W populations, respectively under low-N. Under high-N, ASI reduced by 0.75 days in TZL compl1-W (Table 3).

Effects of recurrent selection and nitrogen level of yield and yield traits of maize

Effect of environment was significant for yield and all other agronomic traits considered in the combined analysis of variance (Table 4). Variances attributable to genotype were significant for yield and yield traits except cob length. $G \times E$ was not significant for yield

Table 1 Soil chemical properties and particle size analysis result for the experimental sites

Chemical properties	Location					
	Ikenne		Ibadan			
	High N	Low N	Low-N	High N-1	High N-2	High N-3
pH (1:1 H ₂ O)	6.2	6.0	6.5	6.3	6.3	6.3
Organic carbon (g kg ⁻¹)	6.3	6.3	6.0	6.1	6.0	6.2
Total N (g kg ⁻¹)	0.10	0.12	0.08	0.08	0.08	0.10
Available P (mg kg ⁻¹)	6.00	6.40	6.10	6.20	6.30	6.50
K (cmol kg ⁻¹)	0.24	0.24	0.28	0.28	0.24	0.26
Ca (cmol kg ⁻¹)	1.80	1.72	2.00	2.25	2.05	2.08
Mg (cmol kg ⁻¹)	1.00	0.92	1.27	1.23	1.12	1.35
Particle size analyses (g kg ⁻¹)						
Sand	820	810	840	830	835	830
Silt	100	100	72	70	75	73
Clay	80	90	88	100	90	97
Textural class (USDA)	<i>LS</i>	<i>LS</i>	<i>LS</i>	<i>LS</i>	<i>LS</i>	<i>LS</i>

LS Loamy sand

Table 2 Means squares of physiological traits of six maize populations evaluated in low-N and high-N environments in Ikenne and Ibadan, Nigeria from 2012 to 2014

Sources of variation	df	Leaf area index	Leaf area ratio (cm ² g ⁻¹)	Leaf area duration (days)	Crop growth rate (g m ⁻² day ⁻¹)	Net assimilation rate (g m ⁻² day ⁻¹)	SPAD readings
Environment (E)	5	1.39**	4431.64**	104.04**	566.00**	57.85**	1197.17**
Low-nitrogen (LN)	1	5.07**	6468.45**	338.14**	348.63**	32.46**	73.79**
High-nitrogen (HN)	3	0.22	4967.27**	49.95**	702.85**	71.52**	1140.32**
Low-N vs. high-N	1	1.22**	787.94**	32.22	372.83**	42.26**	5325.54**
Rep/ environment	18	0.34**	65.03	5.69	92.35**	4.85*	0.10
Genotype (G)	14	1.54**	272.10**	167.22**	73.04**	24.76**	16.05**
G × E	70	0.80**	123.67**	97.68**	87.57**	11.91**	24.98**
G × LN	14	1.38**	104.15**	156.30**	25.86	23.54**	13.21*
G × HN	42	0.67**	116.05**	93.70**	67.18**	9.02**	5.85
G × (LN vs. HN)	14	0.47**	143.20**	76.23**	103.8**	14.50**	36.23**
Error	252	0.12	46.85	13.06	33.89	2.69	4.67

Table 3 Means of physiological traits obtained from the evaluation of different cycles of selection for tolerance to low soil nitrogen (N) in six maize populations at two N levels in Ikenne and Ibadan, Nigeria from 2012 to 2014

Population	Leaf area index		Leaf area duration (days)		Leaf area ratio (cm ² g ⁻¹)	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
Acr 97 TZL Comp1-W	2.68	3.23	33.44	39.23	60.92	51.82
Acr 97 TZL Comp1-W LN C1	2.82	3.26	38.15	44.12	64.46	60.21
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	*	*	<i>ns</i>	*
BR9928 DMRSR C0	2.17	2.86	35.72	35.69	62.10	58.01
BR9928 DMRSR LN C1	2.90	3.37	36.44	37.30	69.07	62.42
<i>Significance of change</i>	*	*	<i>ns</i>	<i>ns</i>	*	*
LNTP-W C3	2.59	3.09	32.07	35.94	49.43	52.64
LNTP-W C4	2.89	3.04	37.82	36.71	50.01	54.41
LNTP-W C5	2.85	3.61	38.85	39.86	58.74	58.58
<i>b-value</i>	0.13	0.26	3.39	1.96	4.66	2.97
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	*	*
LNTP-Y C6	2.64	3.00	34.57	41.19	50.96	46.85
LNTP-Y C7	2.97	3.47	39.43	40.66	56.08	46.06
LNTP-Y C8	3.25	3.87	39.52	43.12	56.39	52.46
<i>b-value</i>	0.31	0.44	2.50	0.96	2.72	3.00
<i>Significance of change</i>	*	*	<i>ns</i>	<i>ns</i>	<i>ns</i>	*
TZPB Prol.C3	2.68	3.35	33.28	37.47	64.05	52.21
TZPB Prol.C4	3.28	3.24	36.54	38.28	61.62	56.34
TZPB Prol. C5	3.37	4.04	42.20	48.14	65.01	56.99
<i>b-value</i>	0.35	0.35	4.46	5.34	0.48	2.39
<i>Significance of change</i>	*	*	*	*	<i>ns</i>	<i>ns</i>
TZL Comp 1-W C6	2.68	3.48	34.75	38.64	58.10	52.61
TZL Comp 1-W C6 LN C1	2.80	3.25	37.92	43.96	63.10	65.71
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	*	*	*	*

Population	Crop growth rate (g m ⁻² day ⁻¹)		Net assimilation rate (g m ⁻² day ⁻¹)		Anthesis-silking interval (days)	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
Acr 97 TZL Comp1-W	14.46	23.93	5.34	8.84	1.50	1.25
Acr 97 TZL Comp1-W LN C1	18.41	26.23	6.05	9.44	1.50	1.25
<i>Significance of change</i>	*	*	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
BR9928 DMRSR C0	14.57	19.00	5.49	6.51	2.00	1.00
BR9928 DMRSR LN C1	15.21	21.60	6.72	7.89	1.25	1.00
<i>Significance of change</i>	<i>ns</i>	*	*	*	*	<i>ns</i>
LNTP-W C3	14.56	19.56	6.23	7.10	1.75	1.50
LNTP-W C4	16.23	22.21	7.42	8.90	1.00	1.00
LNTP-W C5	19.00	23.56	8.50	9.86	1.25	0.75
<i>b-value</i>	2.22	2.00	1.08	1.38	-0.50	-0.25
<i>Significance of change</i>	*	<i>ns</i>	*	*	*	<i>ns</i>
LNTP-Y C6	16.23	18.67	6.99	7.32	1.75	1.25
LNTP-Y C7	17.63	23.45	7.52	8.45	1.25	1.50
LNTP-Y C8	18.00	24.22	7.97	9.23	1.25	1.50
<i>b-value</i>	0.89	2.78	0.49	0.95	0.25	0.13

Table 3 continued

Population	Crop growth rate (g m ⁻² day ⁻¹)		Net assimilation rate (g m ⁻² day ⁻¹)		Anthesis-silking interval (days)	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
TZPB Prol.C3	15.17	20.00	6.71	7.68	1.25	1.50
TZPB Prol.C4	16.23	22.45	7.18	8.43	2.00	1.00
TZPB Prol. C5	18.00	25.15	8.41	9.70	1.50	1.25
<i>b-value</i>	1.42	2.57	0.85	1.01	0.25	-0.25
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
TZL Comp 1-W C6	15.33	22.43	6.28	8.45	1.75	1.75
TZL Comp 1-W C6 LN C1	19.32	26.34	7.56	10.35	1.50	1.00
<i>Significance of change</i>	*	*	*	*	<i>ns</i>	*

ns Not significant

*, ** Significant at 0.05, 0.01 probability levels, respectively

and yield traits except 100 kernel weight but significant genotype X low-N interactions were observed for grain yield, weight of ear per plant and number of ears per plant (Table 4).

Under low-N, significant yield gain was obtained in response to selection from Acr97 TZL Comp1-W, TZPB Prol. and TZLComp1-W. Furthermore, selection increased grain yield in Acr97 TZL Comp1-W, LNTP-W, TZPB Prol. and TZL Comp W-1 under high-N (Table 5). Increases in grain yield obtained in Acr97 TZL Comp1-W, LNTP-W and TZPB Prol were accompanied by significant increases in 100 kernel weight. While yield increases obtained in Acr97 TZL Comp1-W was accompanied by increases in number of kernel rows and kernels per row. In general, nitrogen stress reduced number of kernels per row, one hundred kernel weight and grain yield by 3, 5 and 31% respectively. Increased nitrogen levels shortened ASI by 0.40 days (Table 6).

Relationship among physiological and yield traits

Correlations between physiological and yield traits are presented in Table 7. Highly positive and significant relationship were obtained between 100 kernel weight with leaf chlorophyll (SPAD) at silking ($p < 0.01$) under both low and high nitrogen environments (Table 7). Grain yield was also positively correlated with SPAD readings ($p < 0.05$) at low (0.84*) and high (0.71*) nitrogen levels. Grain yield was positively related to plant biomass recorded at silking at

both high and low nitrogen conditions. Correlation of LAR and grain yield was significant but negative under high nitrogen environments (-0.52^*) but not significant under low nitrogen conditions. There were no significant associations between LAI, LAD with grain yield and agronomic traits in low-N environment. There was a high positive correlation between CGR and grain yield in both low and high-N environments (Table 7).

LAI was positively and significant correlated with LAR (0.63**, 0.67**) and CGR (0.28*, 0.35*) under low and high N conditions respectively while LAR was negatively correlated with CGR, NAR and plant biomass under low and high. No significant relationships were observed between LAI and plant biomass at silking under both high and low-N conditions (Table 8).

Grain yield had positive and significant relationships with number of kernels per row (0.29*, 0.36**) and 100 kernel weight (0.21*, 0.27*) in both high and low-N conditions respectively (Table 9).

Discussion

The identification of morpho-physiological traits responsible for better performance of crops in a target environment is useful for cultivar selection and is crucial in maize improvement. Significance of genotype x N-environment interaction for all physiological traits is an indication that N-fertilizer rates

Table 4 Means squares of yield and yield traits of six maize populations evaluated in low-N and high- N environments in Ikenne and Ibadan, Nigeria from 2012 to 2014

Sources of variation	df	Cob length (cm)	Cob diameter (cm)	Kernel rows	Kernels per row	Ears per plant	Weight of ear/plant (g)	100 kernel weight (g)	Grain yield (mg ha ⁻¹)
Environment (E)	5	55.45**	2.57**	8.28**	569.27**	0.33**	23,979.40**	342.03**	66,274,883.6**
Low-nitrogen (LN)	1	17.00	11.69**	19.92	15.74	1.19**	450.89	156.24**	29,077,725.78**
High-nitrogen (HN)	3	55.73**	1.18**	6.48**	644.35**	0.14**	38,627.68**	451.28**	26,068,189.69**
Low-N vs. high-N	1	93.74**	0.01	2.21	913.23**	0.01	3563.05*	197.59**	224,092,123.1**
Rep/ environment	18	9.18	0.40	1.33	15.78	0.05	1071.29	35.74**	2,489,059.9
Genotype (G)	14	7.82	1.17**	15.40**	30.21**	0.32**	2295.80**	87.07**	3,500,906.8**
G × E	70	6.20	0.38	1.84	17.14**	0.03	631.52	23.68*	1,113,753.8
G × LN	14	12.45	0.87	2.62	8.04	0.05*	960.86**	11.58	1,234,741.86*
G × HN	42	1.66	0.06	1.53	21.95**	0.03	626.17	29.35**	1,100,370.45
G × (LN vs. HN)	14	0.62	0.03	1.20	12.23*	0.02	234.21	21.22*	894,526.87
Error	252	6.94	0.37	1.49	9.95	0.03	540.02	16.11	868,553.0

*, ** Significant at 0.05, 0.01 probability levels, respectively

differentially affected the traits amongst the genotypes. LAI of a crop is an indication of its photosynthetic potential. However, results from the present study revealed that larger leaf area and supposedly higher photosynthetic activity did not necessarily translate to higher grain yield. Hirel et al. (2001) had earlier provided evidence that suggests that increased productivity in maize genotypes was not only due to increased photosynthetic activity by the leaves but also due to the ability to accumulate nitrate in leaves during vegetative growth and to effectively remobilize this stored nitrogen during grain filling.

Recurrent selection, a cyclical procedure designed to increase frequency of favourable alleles in a population has been used by various workers to improve grain yield under different stress conditions including drought (Menkir and Kling 1999), downy mildew infection (Ajala et al. 2003), *Striga* infestation (Menkir and Kling 2007) and stem borer infestation (Ajala et al. 2001). The higher LAD values displayed by improved versions of Acr 97 TZL Comp1-W, TZL Comp 1-W and TZPB Prol. populations revealed that improved populations remained photosynthetically active for a larger portion of the grain filling period. Thus, maintenance of photosynthetically active tissue

for a longer period of time during mid to late grain filling stages of development enabled the improved populations to produce more dry matter used to fill the grain. This result is consistent with those from previous study (Fakorede and Mock 1980) which indicated that high yielding maize genotypes demonstrated longer LADs after anthesis than lower yielding ones.

Maize populations respond differently to different selection procedures due to their genetic composition. Three populations namely LNTP-W, LNTP-Y and TZPB Prol, used in this study were developed primarily for tolerance to low soil nitrogen conditions while the fourth, BR9928DMRSR was equally known a priori to be tolerant to low soil nitrogen. Therefore, the non response of three out of the four populations to further selection under low N is an indication of the saturation of favourable alleles leading to reduced variability for tolerance to low soil nitrogen, a situation that might also occur with the fourth population with further selection. On the contrary, the remaining two populations, Acr97TZLComp-1W and TZLComp-1WC6 were developed to withstand *Striga* spp. infestation and not low nitrogen condition resulting in the observed increase in yield after only

Table 5 Means of yield and yield traits obtained from the evaluation of different cycles of selection for tolerance to low soil nitrogen (N) in six maize populations at two N levels in Ikenne and Ibadan, Nigeria from 2012 to 2014

Population	Cob length (cm)		Ears per plant		No. of kernels per row	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
Acr 97 TZL Comp1-W	16.06	18.10	0.95	1.02	32.42	34.92
Acr 97 TZL Comp1-W LN C1	17.85	18.36	1.04	1.04	34.28	36.37
<i>Significance of change</i>	*	ns	ns	ns	*	*
BR9928 DMRSR C0	17.34	17.14	0.94	1.06	32.87	32.29
BR9928 DMRSR LN C1	17.79	17.52	1.05	0.99	32.83	32.59
<i>Significance of change</i>	ns	ns	ns	ns	ns	ns
LNTP-W C3	17.37	18.54	0.90	1.06	34.06	36.76
LNTP-W C4	17.75	19.05	0.94	1.03	35.16	37.90
LNTP-W C5	19.03	19.38	0.97	1.01	35.99	38.29
<i>b-value</i>	0.83	0.42	0.04	0.03	0.97	0.77
<i>Significance of change</i>	ns	ns	ns	ns	ns	ns
LNTP-Y C6	16.29	16.60	1.00	1.14	33.58	32.71
LNTP-Y C7	17.54	17.63	1.06	1.26	33.61	33.83
LNTP-Y C8	18.46	17.77	1.02	1.15	33.71	33.82
<i>b-value</i>	1.19	0.59	0.01	0.01	0.06	0.57
<i>Significance of change</i>	*	ns	ns	ns	ns	ns
TZPB Prol.C3	16.76	16.64	1.15	1.36	30.33	34.00
TZPB Prol.C4	17.34	18.00	1.29	1.36	32.27	35.67
TZPB Prol. C5	17.96	18.61	1.15	1.36	33.45	35.46
<i>b-value</i>	0.60	0.98	0.00	0.00	1.56	0.73
<i>Significance of change</i>	ns	*	ns	ns	ns	ns
TZL Comp 1-W C6	16.76	17.20	0.96	0.91	31.08	33.50
TZL Comp 1-W C6 LN C1	17.10	17.87	1.04	1.06	32.21	34.25
<i>Significance of change</i>	ns	ns	ns	ns	ns	ns
Population	100 grain weight (g)		Kernel rows		Grain yield (mg ha ⁻¹)	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
Acr 97 TZL Comp1-W	28.75	32.22	13.33	14.83	3.50	5.23
Acr 97 TZL Comp1-W LN C1	30.73	35.17	15.16	16.30	4.27	5.99
<i>Significance of change</i>	*	*	*	*	*	*
BR9928 DMRSR C0	26.60	26.67	12.59	14.16	3.20	4.23
BR9928 DMRSR LN C1	32.16	31.11	14.12	14.17	3.55	4.60
<i>Significance of change</i>	**	**	*	ns	ns	ns
LNTP-W C3	30.07	33.28	13.37	13.54	2.85	4.00
LNTP-W C4	32.00	34.66	14.04	14.17	4.17	5.59
LNTP-W C5	32.11	36.47	13.96	14.58	3.51	5.97
<i>b-value</i>	1.02	1.60	0.34	0.52	0.33	0.96
<i>Significance of change</i>	*	*	ns	ns	ns	**
LNTP-Y C6	29.79	34.62	13.58	13.55	3.50	5.37
LNTP-Y C7	30.30	35.63	13.41	13.77	3.86	5.56
LNTP-Y C8	31.09	35.60	13.67	14.13	3.87	5.42
<i>b-value</i>	0.65	0.49	0.05	0.29	0.19	0.03
<i>Significance of change</i>	ns	ns	ns	ns	ns	ns

Table 5 continued

Population	100 grain weight (g)		Kernel rows		Grain yield (mg ha ⁻¹)	
	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹	45 kg N ha ⁻¹	90 kg N ha ⁻¹
TZPB Prol.C3	29.51	34.20	13.00	13.55	3.23	4.72
TZPB Prol.C4	30.88	35.23	12.93	13.87	4.10	5.13
TZPB Prol. C5	32.92	36.32	14.34	14.68	4.41	5.70
<i>b-value</i>	0.71	0.53	0.67	0.56	0.59	0.50
<i>Significance of change</i>	*	<i>ns</i>	<i>ns</i>	<i>ns</i>	*	*
TZL Comp 1-W C6	29.50	32.43	13.00	14.28	3.06	4.41
TZL Comp 1-W C6 LN C1	30.12	33.25	13.08	15.34	3.52	5.69
<i>Significance of change</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	*	**

ns not significant

*, ** Significant at 0.05, 0.01 probability levels, respectively

one cycle of selection for tolerance to low soil nitrogen.

CGR and SPAD readings were the physiological parameters most associated with grain yield in this study. SPAD is used to measure relative chlorophyll content in plant leaves and it is effectively used to diagnose N status and predict grain yield potential in maize (Vetsch and Randall 2004). SPAD readings obtained in this study had a high and positive relationship with grain yield and 100 kernel weight. Bullock and Anderson (1998) reported no association between maize grain yield and SPAD readings but concluded that SPAD reading can be used as a diagnostic aid for N management in maize. Similarly, Teal et al. (2006) also reported strong association between grain yield and normalized difference vegetative index (NDVI) at between V6 and V8 growth stage of maize, while Inman et al. (2007) reported a strong relationship between grain yield and SPAD readings and NDVI at about the V8–R1 growth stage of maize. More recently, Kante et al. (2016) reported significant correlation between chlorophyll content represented by stay green characteristic with kernel weight at different growth stages beginning from flowering in two temperate maize mapping populations, a similar finding to that reported herein thus indicating the usefulness of SPAD to predict grain yield especially in stressed environments.

The positive and significant association between CGR and grain yield obtained under both low and high N environment was previously reported by Andrade et al. (1999) and Adebo and Olaoye (2010) had also earlier reported that CGR rate during silking is highly

associated with grain yield. Furthermore, the negative, though not significant correlation between number of kernels per row and 100 grain weight agrees with the findings of Borrás and Otegui (2001) that reported an inverse relationship between kernel number and kernel weight and also provided additional explanation that the decrease in kernel weight comes from a reduced kernel fill rate caused by decreased assimilate supply per kernel.

Contradicting results on the growth analysis parameters that significantly affect grain yield obtained from previous studies could perhaps best explain the reason why increase in grain yield of some populations was accompanied by significant changes in some physiological and morphological parameters but not in other populations. While Kumar and Singh (2001) argued that LAI and LAD are important components for determining the dry matter accumulation and grain yield in maize, Adebo and Olaoye (2010) reported that LAI and LAD were not determinants of grain yield in maize and concluded that genotypic superiority for grain yield is not particularly related to differences in any of the two traits but rather dependent on the inherent genetic potential of the varieties. Thus increment in yield in the improved cycles could have been a result of greater abilities of the genotypes to translocate photosynthate from leaves to developing grain as shown by the positive relationship of grain yield with CGR. In effect, CGR is the only physiological parameter that cuts across genotypes and could be used as indirect measurements for improving maize for tolerance to low soil nitrogen amongst the set of parameters utilizing leaf area and plant biomass for computation. It can thus be argued that

Table 6 Effects of nitrogen fertilizer application on agronomic traits of maize populations grown under 45(low-N) and 90(high-N) kg N ha⁻¹ fertilizer at Ikenne and Ibadan, Nigeria from 2012 to 2014

Traits	N-rate			% reduction at low-N
	Low-N Mean	High-N Mean	Level of significance	
Days to anthesis	57.4	57.92	ns	0.89
Days to silking	58.86	59.01	ns	0.25
Anthesis-silking interval (Days)	2.40	2.00	**	-20.00
Plant height (cm)	186.29	192.16	ns	3.05
Ear height(cm)	91.00	95.00	ns	4.20
Kernel rows	13.63	13.72	ns	0.66
Number of kernels per row	33.66	34.82	*	3.33
Ears per plant	1.03	1.11	ns	7.20
One hundred kernel weight (g)	30.05	31.57	**	4.81
Grain yield (mg ha ⁻¹)	3.23	5.10	**	30.68

ns Not significant

*, ** Significant at 0.05, 0.01 probability levels, respectively

Table 7 Correlation coefficients between selected agronomic and yield traits and physiological traits at silking of populations of maize grown under low-N and high-N fertilizer application at Ikenne and Ibadan, Nigeria from 2012 to 2014

	N-level	Plant height (cm)	Anthesis-silking interval (days)	Kernel rows	No. of kernels	100 kernel weight (g)	Grain yield (mg ha ⁻¹)
LAI	Low-N	0.34	-0.15	-0.40 ns	0.09 ns	-0.28 ns	0.08 ns
	High-N	0.11	0.36	-0.16 ns	-0.06 ns	-0.26 ns	0.06 ns
LAR (cm ² g ⁻¹)	Low-N	0.56*	-0.03 ns	0.22 ns	0.33 ns	-0.39 ns	-0.52*
	High-N	0.44*	0.02 ns	-0.38 ns	0.05 ns	0.12 ns	-0.32 ns
LAD (days)	Low-N	0.20 ns	-0.19 ns	-0.02 ns	0.25 ns	-0.22 ns	-0.06 ns
	High-N	0.21 ns	0.06 ns	-0.16 ns	-0.11 ns	-0.16 ns	-0.08 ns
CGR (g m ⁻² day ⁻¹)	Low-N	-0.18 ns	-0.11 ns	-0.21 ns	0.48*	0.29 ns	0.46*
	High-N	0.10 ns	0.16 ns	0.15 ns	0.56*	0.40 ns	0.61**
Total dry weight (g plant ⁻¹)	Low-N	0.32 ns	0.02 ns	-0.12 ns	-0.10 ns	0.47*	0.67**
	High-N	0.57**	0.42 ns	0.21 ns	0.44 ns	0.57*	0.71**
Leaf chlorophyll (SPAD)	Low-N	-0.35 ns	0.15 ns	0.02 ns	-0.08 ns	0.63**	0.84**
	High-N	-0.07 ns	0.10 ns	0.26 ns	0.38 ns	0.66**	0.71**

ns Not significant

*, ** Significant at 0.05, 0.01 probability levels, respectively

plant biomass at silking is not related to grain yield at maturity. Racjan and Tollenaar (1999) had earlier postulated that difference in dry matter accumulation in the ear is attributed to post-silking assimilate uptake. Therefore the significant increases in values in CGR obtained due to selection in some of the populations simply suggest that more cycles of selection will be

required in the other populations to significantly shift values for CGR in the right direction. It is therefore suggested that SPAD values and CGR could be used singly or in combination to aid selection of maize genotypes for tolerance to low soil nitrogen.

The observed 31% reduction in maize grain yield under low-N in this study is comparable to results

Table 8 Correlation coefficients among selected physiological traits of six maize populations at low-N (above the diagonal) and high-N (below the diagonal) at Ikenne and Ibadan, Nigeria from 2012 to 2014

	Leaf area index	Leaf area ratio (cm ² g ⁻¹)	Crop growth rate (g m ⁻² day ⁻¹)	Net assimilation rate (g m ⁻² day ⁻¹)	Plant biomass at silking (g plant ⁻¹)
Leaf area index		0.63**	0.28**	0.14 ^{ns}	0.18 ^{ns}
Leaf area ratio (cm ² g ⁻¹)	0.67**		-0.47***	-0.57***	-0.63**
Crop growth rate (g m ⁻² day ⁻¹)	0.35*	-0.43**		0.96***	0.89***
Net assimilation rate (g m ⁻² day ⁻¹)	0.27*	-0.56**	0.88***		0.87***
Total dry weight (g plant ⁻¹)	0.10 ^{ns}	-0.53***	0.77***	0.90***	

ns Not significant

*, **, *** Significant at 0.05, 0.01, 0.001 probability levels, respectively, n = 68

Table 9 Correlation coefficients among selected agronomic and yield traits of six maize populations at low-N (above the diagonal) and high-N (below the diagonal) application at Ikenne and Ibadan, Nigeria from 2012 to 2014

	Plant height (cm)	Ear height (cm)	Kernel rows	Kernels per row	One hundred kernel weight (g)	Grain yield (mg ha ⁻¹)
Plant height (cm)		0.78***	0.19 ^{ns}	-0.03 ^{ns}	-0.10 ^{ns}	0.29*
Ear height (cm)	0.42***		0.22*	0.01 ^{ns}	-0.15 ^{ns}	-0.14 ^{ns}
Kernel rows	0.07 ^{ns}	-0.03 ^{ns}		0.04 ^{ns}	-0.28*	0.06 ^{ns}
Number of kernels/row	0.16 ^{ns}	0.25*	0.04 ^{ns}		-0.14 ^{ns}	0.29*
100 kernel weight (g)	0.07 ^{ns}	0.08 ^{ns}	-0.21 ^{ns}	-0.16 ^{ns}		0.21*
Grain yield (mg ha ⁻¹)	-0.07 ^{ns}	0.06 ^{ns}	0.02 ^{ns}	0.36**	0.27*	

ns Not significant

*, **, *** Significant at 0.05, 0.01, 0.001 probability levels, respectively, n = 68

obtained by Bertin and Gallais (2000) and Abe et al. (2013) that reported 38 and 35% reduction in maize grain yield under low-N, respectively. Furthermore, the reduction in yield from high to low N environments was accompanied by reduction in Kernel weight as also observed by Muchow (1988) and Bertin and Gallais (2000) but not by Purcino et al. (2000). Yield in maize is primarily due to the number of cobs harvested per plot, while cob yield per se is dependent on kernel weight and number, two parameters that were affected in this study.

Conclusion

Crop growth rate (CGR) and leaf chlorophyll concentration measured by SPAD were the traits most associated with grain yield under low soil nitrogen. The two parameters can thus be used singly or in combination with other desirable agronomic traits to

construct an index for selecting maize for tolerance to low soil nitrogen.

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