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Combining Ability and Gene Action of Tropical Maize (*Zea mays* L.) Inbred Lines under Low and High Nitrogen Conditions

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Abstract

This study was conducted to determine combining ability and gene action in elite maize inbred lines under low and high soil nitrogen conditions for hybrid breeding. Forty two tropical inbred lines (three testers and 39 lines) were crossed using line × tester mating design. The resulting 117 F1 hybrids, along with 4 hybrids used as checks, were evaluated using an 11 × 11 lattice design with two replications for grain yield and yield related traits during the 2012 and 2013 cropping seasons at two sites (Mbalmayo and Nkolbisson). Results revealed predominant additive gene effect under high soil nitrogen (N) conditions. Non-additive gene effect influenced grain yield under low soil and thus could be exploited for hybrid development. Under high N conditions inbred lines CLYN246, J16-1, CLWN201, TL-11-A-1642-5, CLQRCWQ26 and 1368 were good general combiners. Lines CML 343, ATP S6 20-Y-1, CLWN201, 1368, ATP S9 30 Y-1 and CLQRCWQ26 were good general combiners for grain yield under low N. They could be used to develop low N tolerant varieties. Different single cross hybrid combinations were identified for high grain yields under both low and high N conditions. The selected lines and single cross hybrids are a useful source of valuable genetic material for future maize hybrid breeding or direct production under low N.

Keywords: maize, hybrids, low nitrogen, combining ability, line × tester

1. Introduction

Maize (*Zea mays* L.) is one of the most important and widely grown cereal crops in West and Central Africa. In sub-Saharan Africa (SSA), maize is a staple food for an estimated 50% of the population (IITA, 2014) and accounts for about 15% of the calorific intake of the population (Badu-Apraku & Akinwale, 2011). World maize production is estimated at about 872 million tonnes, planted on over 177 million hectares (NUEweb, 2012). African production represents only 7.9% of the world's production. This may be because average maize grain yield in Africa is still low compared to developed countries, especially under small-scale farmers' conditions where many stresses are present.

In Cameroon, despite the increase in maize production from 966,000 tonnes in 2004 to 1,647,036 tonnes in 2013 (FAOSTAT, 2014), there is a deficit between domestic demand and supply. Failure of the national production to meet the needs of Cameroonian households may be attributed to the effects of various biotic and abiotic constraints including low soil fertility, soil acidity, poor crop management practices, low adoption of improved varieties, and pest and disease damages (Ngoko et al., 2002; Nguimgo et al., 2003; The et al., 2013). Low soil fertility, particularly soil nitrogen deficiency, is a serious concern of maize farmers in Cameroon (Hauser & Nolte, 2002; Ngoko et al., 2002; Nguimgo et al., 2003; The et al., 2013). The problem is worsened by the lack of availability and/or high prices of mineral fertilizers in the country. In addition, continuous cropping over decades with no measures in place to regenerate the soil's productivity has contributed to decreased soil fertility and, consequently, the low level of maize production in Cameroon.

One effective strategy to reduce fertilizer requirements is to develop maize genotypes with high nitrogen use efficiency and high yield potential. Genotypes with high yield potential are also needed to support the rapidly growing population and may provide incentives to farmers who are trying to make modest increase in nitrogen application in their maize fields.

In maize breeding programs, analysis of general combining ability (GCA) and specific combining ability (SCA) are essential to identify best inbred lines for hybrid development and hybrid combinations with better specific combining ability (Abrha et al., 2013; Girma et al., 2015). Combining ability is an effective tool which gives useful genetic information for the choice of parents in terms of their performance in series of crosses (Sprague & Tatum, 1942). The development of inbreds having high combining abilities has a fundamental role in the efficient use of heterosis (Vasal et al., 1992). Crossing between inbred lines with high specific combining ability can improve tolerance to different stresses and superior hybrids with high yield production under stress condition (Betràn et al., 2003; Vasal et al., 1997).

Various biometrical approaches are available to assess the breeding value of potential parents and to assess the genetics of the traits of interest. Line × tester analysis (Kempthrone, 1957) is an approach often employed to understand the genetic basis of a given character and combining ability of parents and hybrids (Tamilarasi et al., 2010). The line × tester analysis has been widely used by plant breeders. It is used to breed both self and cross pollinated plants as well as estimating favourable parents, crosses and their general and specific combining ability (Aly, 2013; Majid et al., 2010). It is useful in deciding the relative ability of female and male lines to produce desirable hybrid combinations (Kempthrone, 1957) and also provides information on genetic components. It enables breeders to choose appropriate breeding methods for hybrid varieties or cultivar development programmes. This design has been efficiently used for estimating breeding values of maize inbred lines and for determining the gene action that controls quantitatively inherited traits (Sofi & Rather, 2006) such as low N tolerance.

Genetic studies have been conducted on maize genotypes under low N using different sources of genetic material (Badu-Apraku et al., 2013; Betràn et al., 2003; De Souza et al., 2008; Makumbi et al., 2011; Meseka et al., 2006; Meseka et al., 2013; Miti, 2007; Pswarayi & Vivek, 2008). However, information on gene action conditioning grain yield under low N has been contradictory. The contradictory results obtained by researchers might be due to the N stress level (testing environments) under which the genotypes were tested and/or genotypic differences among sets of genotypes used in the studies (Mosisa, 2008). Many of these studies were conducted using extra early maturing maize lines. Further studies are therefore necessary in order to examine the genetic effects conditioning grain yield and other traits under both low and high N conditions using lines with intermediate maturity cycle. Moreover, the Cameroonian National Maize Breeding Program, in collaboration with the International Institute of Tropical Agriculture (IITA), has developed maize inbred lines adapted to the different agro-ecological zones of Cameroon and to different stresses such as acid soils, drought and Striga. However, very little work has been done on low soil nitrogen. Futhermore, inbreds from IITA, CIMMYT and some African breeding programs have been introduced and there is need to use the national and these newly introduced maize inbreds in studies for combining ability and heterosis in relation to interesting traits under low soil nitrogen and optimum growing conditions.

This study was conducted to identify high yielding hybrids tolerant to low N soils, determine the combining abilities and mode of gene action of intermediate maturing inbred lines for hybrid development under low soil N conditions.

2. Materials and Methods

2.1 Plant Material

Forty-two intermediate to late maturating inbred lines (39 lines and 03 testers) were used in the study. These lines were provided by IRAD Cameroon, IITA and CIMMYT (Table 1). Thirty-nine inbred lines were crossed with three testers (87036, Exp1 24 and 9071) in a line × tester scheme to obtain 117 hybrid combinations. In addition, 4 hybrids (87036 × Exp1 24, 9071 × Exp1 24, 87036 × 9071 and 88069 × Caminbgp$_1$17) were included as checks to make a total of 121 entries. The hybrid 87036 × Exp1 24 is a high yielding hybrid released in Cameroon and adapted to the Humid Forest Zone of Cameroon. Exp1 24 × 9071 is also a high yielding hybrid, developed from a cross between tropical lowland × temperate converted inbreds.

2.2 Experimental Sites

The study was conducted at two locations of the Humid Forest Zone with bimodal rainfall, namely Nkolbisson and Mbalmayo. Nkolbisson is located at 11°36′ E and 3°44′ N, 5 km from the main capital city 'Yaoundé'. The altitude is 650 m above sea level (asl). The annual rainfall is 1560 mm with bimodal distribution. The average daily temperature is 23.5 °C. The soil is sandy clay with pH (water) of 4.52, CEC of 4.79 Cmol (+) kg^{-1} and AL of 0.30 Cmol (+) kg^{-1}. The main cropping system is maize/groundnut/cassava as sole cropping or mix cropping (The et al., 2013).

Mbalmayo is located at 11°30′ E and 3°31′ N, 45 km from Yaounde. The altitude is 641 m asl. The mean annual rainfall varies from 1017 to 1990 mm with bimodal distribution. The mean monthly temperature varies from 25 °C to 22 °C. The soil is sandy clay. The agricultural practice is based on shifting cultivation techniques. The main crops are cassava and cocoyam grown as sole or intercropped with groundnut or maize (Tchienkoua, 1996).

2.3 Site Preparation and Soil Analysis

Low N plots were established by soil depletion of available nitrogen. Soil N depletion consisted of planting maize uniformly in the field at a very high density without any fertilizer application for many growing seasons.

Soil samples collected from the two locations before each cropping season were analyzed for selected physical and chemical properties at the soil laboratory of the International Institute of Tropical Agriculture (IITA) Cameroon.

2.4 Experimental Design and Management

The 121 F_1 hybrids were evaluated during 2012 and 2013 in three cropping seasons under high N level (100 kg ha^{-1}) and low N (20 kg ha^{-1}). At each N level, the 121 hybrids were arranged in an 11 × 11 lattice design. The experimental unit consisted in a single row of 5 m at Mbalmayo and single 4 m at Nkolbisson. Hybrids were planted in 2 replications. The spacing between rows was 0.75 m and 0.5 m between hills within a row. Three seeds were planted in a hill and thinned after emergence to 2 plants, for a final density of 53,330 plants per hectare.

Split fertilization was done on each plot. On the low N plot, the first application in kg ha^{-1} consisted of 10 N, 24 P_2O_5 per hectare and 14 K_2O per hectare, 10 days after planting, and the second dose consisted of 10 N, applied 30 days after planting. On the high N plot, the first application consisted of a mixture of 35 N, 24 P_2O_5 and 14 K_2O per hectare, applied 10 days after planting and the second dose was 65 N per hectare, applied 30 days after planting. The trials were kept clean of weeds throughout the growing cycle by spraying an herbicide with active ingredient 750 g/kg of Atrazine and 40 g/kg of Nicosulfuron at the early stage of maize growth, and later by hand weeding.

2.5 Data Recorded

The various characteristics were recorded viz. anthesis date (AD) and silking date (SD) were recorded as 'number of days after planting', when 50% of plants were shedding pollen and silking, respectively. The anthesis-silking interval (ASI) was calculated as silking date minus anthesis date. Leaf chlorophyll content (%) was determined in four randomly selected plants from each experimental unit and two measurements were obtained per plant on the ear leaf, using a portable Minolta chlorophyll meter (SPAD-502, MINOLTA) one week after silking.

Ear leaf area was determined after silking from the leaf immediately below the upper ear on four randomly selected plants in each plot, and was obtained by multiplying maximum leaf width by leaf length by 0.75 (Montgomery, 1911; Giauffret et al., 1997). Leaf senescence was scored 10 and 12 weeks after planting on a scale from 0 to 10, dividing the percentage of the estimated total leaf area below the ear that is dead by 10. A score of 1 = less than 10% dead leaf and 10 = more than 90% dead leaf. Plant height was measured as the distance from the base of the plant to the height of the first tassel branch.

At harvest, the number of ears per plant was computed as the proportion of total number of ears divided by the number of plants harvested in each experimental unit. Ear aspect was scored on a scale of 1 to 5, where 1 corresponded to clean, uniform, large, and well-filled ears and 5 was the rotten, variable, small, and partially filled ears. At maturity, each row was harvested separately and ear weight was measured for each plot. Grain yield adjusted to 15% grain moisture was calculated in kg ha^{-1} for every entry from the data of fresh ear weight per plot under high N. On low N plots, grain yield was computed from shelled grain weight.

2.6 Statistical Analysis

The data collected were analyzed using general linear model (GLM) procedure in SAS (SAS institute, version 9.2, 2008). Entry means adjusted for block effects were analyzed according to lattice design (Cochran & Cox, 1960). Each environment was defined as year × season × site × nitrogen treatment. The analysis of variance (ANOVA) for each environment and the combined ANOVA were computed with PROC GLM procedure in SAS using the RANDOM statement with the TEST option. Environment effects were treated as random effects and genotypes as fixed effects. The effects of environment on all the measured traits were evaluated through different interaction estimates. Line × tester analysis (Kempthrone, 1957) was done for low N environments, high and across environments to partition the mean square due to crosses into lines, testers and line × tester interaction effects for traits that showed significant differences among crosses. This analysis was done with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS 2008). The relative importance of GCA versus SCA on progeny performance was calculated as the ratio between sum of squares due to GCA or SCA and total sum of squares (GCA and SCA sums of squares) (Beck et al., 1990; Pswarayi & Vivek, 2008).

3. Results

3.1 Analysis of Variance and Hybrid Mean Performance

Across the ten research environments, highly significant differences ($p < 0.01$) were observed among the hybrids and between environments for all the measured traits. Hybrid × environment interaction was significant for all traits suggesting that the relative performance of a hybrid was not consistent across environments.

Under low N environments, significant differences were observed among the hybrids for all traits. The differences between all low N environments were significant ($p < 0.05$) for grain yield and ear leaf chlorophyll content and highly significant for days to silking, anthesis-silking interval, leaf area and plant height. Across low N environments, grain yield ranged from 1539.3 kg ha^{-1} (CML 358 × 9071) to 3770.51 kg ha^{-1} (TL-11-A-1642-5 × Exp1 24), with a mean of 2721.9 kg ha^{-1} (Table 2). Days to silking ranged from 62.50 to 71.70 with a mean of 66.98 days. Anthesis-silking interval ranged from 1.9 days to 4.9 days with a mean of 3.18 days. Leaf area varied from 404.93 to 626.59 cm^2 with a mean of 525.59 cm^2. Leaf chlorophyll content varied from 31.50% to 46.22%, with a mean of 40.80% and higher values were observed among the 20 best hybrids. Mean for plant height was 163.46 cm, ranging from 135 cm to 182.92 cm and ear aspect ranged from 2.35 to 4.05 with a mean of 3.05 (Table 2). Across low N environments, five hybrids yielded more than 3500 kg.ha^{-1}. These were TL-11-A-1642-5 × Exp1 24 (3770.51 kg ha^{-1}), CLWN201 × 87036 (3609.2 kg ha^{-1}) ATP S6 20 Y-2 × Exp1 24 (3556.47 kg ha^{-1}), J16-1 × Exp1 24 (3516.41 kg ha^{-1}), ATP S9 30 Y-1 × Exp1 24 (3514.44 kg ha^{-1}), CLYN246 × 87036 (3512.06 kg ha^{-1}) (Table 2). The two highest yielding hybrids were TL-11-A-1642-5 × Exp1 24 and CLWN201 × 87036 with mean grain yields of 3770.51 kg ha^{-1} and 3609.2 kg ha^{-1} respectively. None of the four hybrid checks figured among the 20 best hybrids under low N.

On the other hand, mean yield varied under high N environments from 3026.5 kg ha^{-1} for J18-1 × 9071 to 6588.8 kg ha^{-1} for TL-11-A-1642-5 × 87036, with an overall mean of 4887.18 kg ha^{-1} (Table 3). Days to 50% silking ranged from 61.2 to 60.40 with a mean of 62.4 days. Mean anthesis-silking interval varied from 1.6 to 3.1 days with a mean of 2.26 days (Table 3). Leaf area ranged from 472.70 cm^2 to 772.06 cm^2 with a mean of 630.63 cm^2. Chlorophyll concentration varied from 43.02% to 55.90% with a mean of 49.96%. Mean of plant height was 182.27, ranging from 153.23 to 210.07 cm. Mean of ear aspect ranged from 1.85 to 3.50, with a mean of 2.5 (Table 3). Five hybrids yielded more than 6000 kg ha^{-1} under high N. These are TL-11-A-1642-5 × 87036 (6588.84 kg ha^{-1}), CLYN246 × 87036 (6584.97 kg ha^{-1}), TZ-STR-133 × 87036 (6393.32 kg ha^{-1}), CLWN201 × Exp1 24 (6152.26 kg ha^{-1}) and J16-1 × Exp1 24 (6048.74 kg ha^{-1}) (Table 3). The highest yielding checks among the four evaluated were 87036 × Exp1 24 (5169.43 kg ha^{-1}) and Exp1 24 × 9071 (5262.24 kg ha^{-1}) but these hybrids were not among the 20 best hybrids selected under high N conditions.

Line x tester analysis revealed highly significant ($p < 0.01$) line general combining ability (GCA) mean squares for all traits under low N environments, (Table 4). Means squares of tester GCA were significantly different for all traits except days to silking and anthesis-silking interval. There were highly significant differences between specific combining ability (SCA) mean squares for all traits except leaf senescence and plant height (Table 4). More still, the contribution of SCA to the total sum of squares of crosses under low N was higher compared to the contribution of GCA for grain yield, anthesis-silking interval, leaf chlorophyll content and ear aspect, while contribution of SCA was lower than GCA for days to silking, leaf senescence and plant height (Table 4).

Under high N conditions, line × tester analysis, revealed significant ($p < 0.05$) line GCA mean squares for anthesis-silking interval and highly significant ($p < 0.01$) line GCA values for all the other measured traits (Table 5). Meanwhile, tester GCA mean square was significant for all traits except anthesis-silking interval (Table 5). SCA mean squares were significant for grain yield, days to silking, leaf area and ear aspect. The contribution of GCA effect to the sum of squares of crosses was higher than the contribution of SCA for all traits except anthesis-silking interval (Table 5).

3.2 General Combining Ability Effects

Six lines had positive, significant GCA effects for grain yield. These are CML 343 (522.26), ATP S6 20-Y1 (504.46), CLWN201 (483.80), 1368 (468.23), ATP S9 30 Y-1 (436.48) and CLQRCWQ26 (396.45) (Table 6). The line with the best GCA effects for grain yield was CML 343. The desired line GCA value for days to silking and anthesis-silking was negative, therefore, the best line for GCA for days to silking were V 351-1/6 and CLA 17 with a GCA effect of -3.23 and -2.46, respectively. The same lines V351-1/6 and CLA 17 had the best GCA effects for anthesis-silking interval (-0.81 and -0.58 respectively). The two best combiners for leaf area, with positive significant GCA effects, were CLQRCWQ26 (43.97) and ATP S5 31-Y-2 (35.98). Moreover, the lines with best GCA for plant height were ATP S9 30 Y-1 (9.31) and 5012 (8.10). For ear aspect, three lines had the best GCA of -0.2. These are CLWN 201, CLYN246 and ATP S6 20 Y-2. Two out of the three testers had positive GCA effects for grain yield under low N. These are 87036 (72.19) and Exp1 24 (59.95). The tester 9071 had a negative GCA value (Table 6).

For days to silking, only 9071 had negative GCA effect (-0.07) while for anthesis-silking interval, 87036 and Exp1 24 had negative GCA (-0.02 and -0.11, respectively), indicating good general combining ability for this trait under low N. The testers 87036 and Exp1 24 also had positive GCA effects for ear leaf area indicating good combining ability for this trait while 9071 GCA effect was negative. For leaf chlorophyll content, 87036 had the best GCA (0.81) while for leaf senescence EXP1 24 was the tester with best GCA (-0.18). For plant height, the tester 87036 had the best GCA (6.75). The testers 87036 (-0.06) and Exp1 24 (-0.06) both had a good GCA effect for ear aspect (Table 6). Under high N conditions, the six best lines with positive, significant GCA effects for grain yield were CLYN246 (982.75), J16-1 (728.75), CLWN201 (720.74), TL-11-A-1642-5 (675.86), CLQRCWQ26 (640.10) and 1368 (546.51) (Table 6).

3.3 Specific Combining Ability Effects for Grain Yield

The cross between line ATP S6 20 Y-2 and Exp1 24 had the highest positive SCA effect (679.45) for grain yield under low N environments (Table 6). This cross was followed by TL-11A-1642-5 × Exp1 24 (648.39) and CML 494 × 9071 (626.40). The first two crosses, ATP S6 20 Y-2 × Exp1 24 and TL-11-A -1642- 5 × Exp1 24, with the best SCA effects, were among the highest yielding hybrids. However, the third best cross CML494 × 9071 and other crosses such as CML358 × Exp1 24, M131 × 9071 were among crosses with highest SCA for yield but they were not among the highest yielding hybrids. Moreover, 1368 × Exp1 24 and ATP S6 20 Y-1 × 87036 had negative SCA (-114,1 and -98 respectively) but yielded more than 3000 kg ha^{-1} while many other crosses with high positive SCA did not yield up to this level. Under high N environment, the best crosses with the highest positive SCA effects were 4001STR × 9071 (986.82), followed by J18-1 × 87036 with an SCA of 905.58 and TZ-STR-133 × 87036 with 893.04 as SCA (Table 6). All these were high yielding hybrids, with two of them (TZ-STR-133 × 87036 and 4001STR × 9071) being among the 20 best yielding under high N conditions.

Table 1. Origin, grain colour and main characteristics of maize inbred lines, testers and hybrid checks used in the study

No	Lines	Origin	Grain color	Main characteristics
1	Cla 17	CIMMYT	Y	Tolerant to acid soils. Heterotic to Cla 18
2	9450	IITA	Y	Converted from B73 and tolerant to low N
3	1368	IITA	W	Extracted from pop 21
4	M 131	IRAD	W	Mid altitude adaptation and tolerant to low N.
5	88094	IRAD	W	Mid altitude adaptation and tolerant to low N.
6	J18-1	WACCI	W	Tolerant to drought
7	88069	IRAD	Y	Mid altitude converted to lowland adaptation.
8	Entrada 29	CIMMYT	W	Tolerant to Aluminium.
9	CML 358	CIMMYT	Y	Tolerant to Aluminium.
10	Entrada 3	CIMMYT	W	Tolerant to Aluminium.
11	CML 254	CIMMYT	W	Tolerant to Aluminium.
12	5012	IITA	W	Temperate converted to tropical adaptation.
13	Cam inb gp1 17	IRAD	Y	Tolerant to acid soil
14	9848	IITA	Y	Temperate converted to tropical adaptation.
15	CLA 18	CIMMYT	Y	Tolerant to Al acid soil.
16	ATP S9 30 Y-1	IRAD	Y	Extracted from acid tolerant maize population.
17	ATP S5 26 Y-1	IRAD	Y	Extracted from acid tolerant maize population.
18	KU1414	IITA	Y	Tolerant to low N
19	5057	IITA	W	Temperate line converted: Susceptible to drought, striga.
20	ATP S6 20 Y-1	IRAD	Y	Extracted from acid tolerant maize population.
21	ATP S8 30 Y-3	IRAD	Y	Extracted from acid tolerant maize population.
22	TZMI 102	IITA	W	
23	J16-1	CIMMYT	W	Tolerant to drought
24	CLYN246	CIMMYT	Y	Tolerant to low N
25	CML395	CIMMYT	W	Susceptible to low N
26	CML494	CIMMYT	W	Susceptible to low N
27	CML165	CIMMYT	Y	Susceptible to low N
28	CLQRCWQ26	CIMMYT	W	Susceptible to low N
29	CML451	CIMMYT	W	Susceptible to low N
30	V-351-1/6	CIMMYT	W	Drought tolerant
31	V-481-73	CIMMYT	W	Drought tolerant
32	TZ-STR-133	IITA	W	
33	TL-11-A-1642-5	CIMMYT	W	
34	Ku 1409	IITA	Y	Tolerant to low N and downy mildew. From Swan pop
35	ATP S6-20-Y-1	IRAD	Y	Extracted from acid tolerant maize population.
36	CLWN201	CIMMYT	W	Tolerant to low N
37	CML444	CIMMYT	W	Tolerant to low N
38	CML343	CIMMYT		Tolerant to low N
39	4001STR	IITA	Y	Tolerant to low N, extracted from population 28
Testers				
40	87036	IRAD	W	Mid altitude line converted to low-land
41	Exp1 24	IRAD	W	Tuxpeno background. Good combiner.
42	9071	IITA	W	Converted from N28 and good combiner

Note. W = white; Y = yellow; IITA = International Institute of Tropical Agriculture; CIMMYT = International Centre for Maize and Wheat Improvement.

Table 2. Means for grain yield and other agronomic traits of selected best 20 hybrids and checks in low N environments

Hybrids	YIELD (kg ha^{-1})	DTS (days)	ASI (days)	LAREA (cm^2)	CHLORO (%)	LSENE (1-9)	PHT (cm)	EA (1-5)	Index (%)
TL-11-A-1642-5 × Exp1 24	3770.51	66.70	2.60	531.77	41.47	2.90	155.78	2.40	30.42
CLWN201 × 87036	3609.2	66.10	4.20	504.41	41.62	3.80	175.60	2.35	33.51
ATP S6 20 Y-2 × Exp1 24	3556.47	64.50	2.90	589.33	41.85	3.20	158.67	2.70	31.00
J16-1 × Exp1 24	3516.41	65.70	3.80	601.41	39.95	3.20	162.07	2.55	41.87
ATP S9 30 Y-1 × Exp1 24	3514.44	66.40	3.10	585.44	44.16	3.70	167.13	2.50	22.04
CLYN246 × 87036	3512.06	65.00	2.70	602.02	41.42	3.28	173.73	2.65	46.67
ATP S9 30 Y-1 × 87036	3464.15	66.60	2.70	536.29	41.98	3.70	179.73	2.95	33.34
CLWN201 × Exp1 24	3415.18	65.30	2.50	491.70	41.09	3.50	153.90	2.75	44.49
ATP S6-20-Y-1 × Exp1 24	3365.33	64.00	2.70	556.50	34.25	3.40	162.90	2.90	40.60
Entrada 29 × Exp1 24	3321.12	66.20	3.30	594.61	42.86	2.85	174.23	2.50	34.40
CML165 × 87036	3319.69	66.50	3.10	585.71	44.38	3.60	174.97	2.60	36.83
1368 × 87036	3315.63	66.70	3.50	574.84	41.11	3.45	173.83	2.65	44.03
CML343 × 87036	3306.36	68.50	2.60	568.73	43.41	3.25	172.00	2.95	40.59
4001STR × 87036	3290.93	66.50	3.20	543.45	43.25	3.60	163.67	2.80	41.08
CLQRCWQ26 × 87036	3288.68	64.70	2.90	558.68	38.54	3.55	169.83	2.70	39.60
CML 444 × Exp1 24	3275.13	71.70	2.60	529.34	40.32	3.65	160.80	3.05	34.98
V-481-73 × Exp1 24	3255.76	68.90	3.60	559.71	44.10	2.60	165.10	2.63	27.28
CML343 × Exp1 24	3242.41	68.20	3.60	527.04	40.78	3.25	160.63	2.75	32.53
Cam inb gp1 17 × 87036	3227.94	66.00	3.70	556.25	37.12	3.40	169.90	2.65	43.77
CML343 × 9071	3224.32	69.00	2.50	509.90	41.94	3.60	171.08	2.75	41.72
Best checks									
87036 × Exp1 24	2866.47	69.90	3.70	521.43	43.03	3.45	175.10	2.75	
Exp1 24 × 9071	2336.64	67.30	2.70	548.51	37.71	3.90	160.15	3.10	
Mean	**2721.49**	**66.98**	**3.18**	**525.59**	**40.80**	**3.53**	**163.46**	**3.05**	
Min	**1539.3**	**62.50**	**1.90**	**404.93**	**31.50**	**2.60**	**135.00**	**2.35**	
Max	**3770.5**	**71.70**	**4.90**	**626.59**	**46.22**	**4.40**	**182.92**	**4.05**	
LSD (0.05)	**1687.9**	**5.32**	**2.42**	**152.05**	**9.51**	**1.53**	**30.42**	**1.07**	

Note. *, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, not significant; DTS = days to 50% silking; ASI = anthesis-silking interval; LAREA = Ear leaf area; CHLORO = leaf chlorophyll content; LSENE = leaf senescence PHT = plant height; EA = ear aspect, YIELD = grain yield.

Table 3. Means for grain yield and other agronomic traits of best 20 hybrids and checks under high N

Hybrids	YIELD (kg ha^{-1})	DTS (days)	ASI (days)	LAREA (cm^2)	CHLORO (%)	PHT (cm)	EA (1-5)
TL-11-A-1642-5 × 87036	6588.84	65.20	1.70	650.86	51.08	193.57	2.40
CLYN246 × 87036	6584.97	63.40	2.20	740.32	54.19	197.70	2.05
TZ-STR-133 × 87036	6393.32	62.50	2.50	582.73	51.64	194.03	2.40
CLWN201 × Exp1 24	6152.26	63.10	2.00	617.83	49.52	174.17	2.05
J16-1 × Exp1 24	6048.74	63.00	2.20	652.95	47.84	174.97	2.10
CLQRCWQ26 × Exp1 24	5968.82	64.90	2.30	606.80	47.04	174.40	2.10
1368 × 87036	5923.65	64.30	2.00	625.94	48.64	195.30	2.10
CLA 18 × Exp1 24	5909.70	64.20	2.00	635.94	48.63	168.81	2.05
4001STR × 9071	5792.07	63.00	2.20	645.79	48.67	177.80	2.45
J16-1 × 87036	5780.49	63.70	1.90	654.25	51.02	181.73	2.30
CML395 × Exp1 24	5772.47	66.30	2.10	656.09	45.69	177.13	2.35
ATP S6-20-Y-1 × 87036	5765.88	63.60	1.60	671.13	52.65	198.03	1.90
Cam inb gp1 17 × 87036	5741.05	64.60	2.90	614.06	55.90	196.33	1.85
CML451 × 87036	5729.07	66.30	2.70	616.98	47.88	187.50	2.45
CLYN246 × Exp1 24	5708.79	63.40	2.10	677.84	50.52	175.92	2.15
CML 358 × 87036	5699.02	65.60	2.30	644.87	46.79	197.07	2.40
CLA 18 × 87036	5694.14	64.20	2.20	663.14	54.10	199.67	2.15
88069 × 9071	5687.94	62.30	2.40	709.45	53.63	188.73	2.40
ATP S5 31 Y-2 × 87036	5682.27	63.50	2.30	639.69	51.14	180.47	2.40
ATP S6-20-Y-1 × Exp1 24	5665.37	63.60	2.10	668.94	47.33	178.10	2.30
Best checks							
87036 × Exp1 24	5169.43	64.60	2.50	655.17	49.73	185.60	2.35
Exp1 24 × 9071	5262.24	68.20	2.10	680.24	47.74	176.23	2.90
Mean	**4887.18**	**64.73**	**2.26**	**630.63**	**49.96**	**182.27**	**2.50**
Min	**3026.50**	**61.20**	**1.60**	**472.70**	**43.02**	**153.23**	**1.85**
Max	**6588.80**	**69.40**	**3.10**	**772.06**	**55.90**	**210.07**	**3.50**
LSD (0.05)	**2236.60**	**4.89**	**1.48**	**176.02**	**9.82**	**34.55**	**0.93**

Note. *, **, Significant at 0.05 and 0.01 probability levels, respectively, and ns, not significant; DTS = days to 50% silking; ASI = anthesis-silking interval; LAREA = Ear leaf area; CHLORO = leaf chlorophyll content; PHT = plant height; EA = ear aspect, YIELD = grain yield.

Table 4. Line × tester analysis for grain yield and agronomic traits across low N environments and percentage contribution of GCA and SCA to the total sum of squares

Source of variation	**df**	**YIELD (kg ha^{-1})**	**DTS (days)**	**ASI (days)**	**LAREA (cm^2)**	**CHLORO (%)**	**LSENE (1-9)**	**PHT (cm)**	**EA (1-5)**
Env	4	115584228.4*	2565.56**	150.00**	916162.69**	12249.75*	64.57ns	130530.30**	2.24ns
Rep (Env)	5	18845743.3**	57.41ns	4.42ns	59773.79ns	2075.55**	26.63**	1803.32ns	2.93*
Crosses	116	1604070.5**	21.31**	2.46**	13004.16**	61.88**	1.06**	660.13**	0.84**
Env × Crosses	464	1281639.8**	9.30*	1.91*	9364.79**	31.93*	0.75*	395.42**	0.47**
Line (GCA)	38	2033201.1**	38.82**	3.40**	17208.56**	67.92**	1.32**	629.38**	1.06**
Tester (GCA)	2	6836645.8**	0.94ns	4.11ns	16265.33ns	305.68**	10.93**	13490.22**	3.44**
Line × Tester (SCA)	76	1227344**	11.58**	2.08*	11138.17**	48.92**	0.71ns	317.82ns	0.64**
Env × Line (GCA)	152	1586891.9**	8.83ns	2.18**	9477.26**	37.02**	0.79*	365.82*	0.62**
Env × Tester (GCA)	8	1824558.9*	24.08**	1.15ns	15949.62*	59.08**	1.03ns	1509.20**	0.48ns
Env × Line × Tester (SCA)	304	1095883.3**	9.16*	1.74ns	8863.19**	27.85ns	0.72ns	365.70**	0.39**
Error	689	770917	7.56	1.53	6477.74	25.99	0.62	283.15	0.3
%GCA SS (Line)		41.52	64.95	44.38	43.35	35.96	40.99	31.23	41.26
%GCA SS (Tester)		7.35	0.11	2.88	2.16	8.52	17.84	35.23	7.03
%SCA SS (Line × Tester)		50.13	35.48	55.34	56.12	51.80	43.92	31.54	49.40

Note. *, **, Significant at 0.05 and 0.01probability levels, respectively, and ns, not significant; DTS = days to 50% silking; ASI = anthesis-silking interval; LAREA = Ear leaf area; CHLORO = leaf chlorophyll content; LSENE = leaf senescence PHT = plant height; EA = ear aspect, YIELD = grain yield; GCA = general combining ability; SCA = specific combining ability; SS = sum of squares.

Table 5. Line × tester analysis for grain yield and other agronomic traits across high N environments and percentage contribution of GCA and SCA to the total sum of squares

Source of variation	**df**	**YIELD (kg ha^{-1})**	**DTS (days)**	**ASI (days)**	**LAREA (cm^2)**	**CHLORO (%)**	**PHT (cm)**	**EA (1-5)**
Env	4	113613785.2*	152.37ns	14.48**	1253297.66**	707.94ns	158316.66*	4.12ns
Rep (Env)	5	23958606.9**	63.79**	0.57ns	91730.79**	189.13*	26106.28**	2.19**
Crosses	116	4235566.4**	18.05**	0.72ns	18531.24**	41.88**	877.13**	0.87**
Env *Crosses	464	1840627.2**	10.11**	0.59ns	13091.60**	30.38*	461.43**	0.040**
Line (GCA)	38	5735295**	31.32**	0.92*	27262.50**	50.34**	864.85**	1.10**
Tester (GCA)	2	27425796**	52.36**	0.95ns	33483.60*	608.21**	17622.32**	4.5**
Line*Tester (SCA)	76	2766032.3**	9.89**	0.61ns	13372.88*	22.97ns	401.10ns	0.67**
Env*Line (GCA)	152	2297712.1**	11.97**	0.57ns	16689.71**	30.84ns	492.73**	0.39**
Env*Tester (GCA)	8	3273204.3*	12.61**	0.94ns	9156.18ns	104.76**	1552.15**	0.58*
Env*Line*Tester (SCA)	304	1502318.4ns	8.68**	0.59ns	11064.99ns	28.46ns	403.81ns	0.40**
Error	689	1292975	6.13	0.57	9877.4	26.3	360.33	0.24
%GCA SS (Lines)		44.36	56.68	42.15	48.19	39.38	32.30	41.24
%GCA SS (Testers)		11.16	4.98	2.31	3.12	25.04	34.64	8.88
%SCA SS (Line × Tester)		42.79	35.78	55.45	47.28	35.93	29.96	49.88

Note. *, **, Significant at 0.05 and 0.01 probability levels, respectively, and ns, not significant; DTS = days to 50% silking; ASI = anthesis-silking interval; LAREA = Ear leaf area; CHLORO = leaf chlorophyll content; PHT = plant height; EA = ear aspect, YIELD = grain yield; GCA = general combining ability; SCA = specific combining ability; SS = sum of square.

Table 6. Specific combining ability effects for grain yield and GCA effects of lines and testers under low and high N environments

Lines	Low N environments				High N environments			
	Testers			GCA lines	Testers			GCA lines
	87036	**Exp1 24**	**9071**		**87036**	**Exp1 24**	**9071**	
Cla 17	-157	156.12	0.88	-235.01	198.45	293.24	-491.69	-197.43*
9450	176.14	-36.55	-139.59	-865.88**	97.77	532.12	-629.89	-880.92*
1368	39.78	-114.17	74.4	468.23*	-45.03	101.87	-56.84	546.51*
M 131	-314.4	-141.49	455.89	-471.41*	-893.42*	301.29	592.13	-867.08**
88094	309.16	-494.04	184.88	-262.54	84.79	-471.23	386.44	-569.49*
J18-1	196.68	-317.1	120.42	-355.27	905.58*	-65.83	-839.75*	-650.35**
88069	-39.04	-90.83	129.87	275.61	-569.85	93.37	476.48	367.32
Entrada 29	-721.19*	452.43	268.76	-215.15	-498.58	358.29	140.28	-501.27*
CML 358	16.68	506.33	-523.02	-321.81	570.35	394.44	-964.79*	-146.94
Entrada 3	265.88	-131.26	-134.62	-158.03	138.63	-330.23	191.6	-470.78*
CML 254	162.89	-62.79	-100.1	19.99	-643.06	508.75	134.32	84.29
5012	-116.73	110.06	6.68	-103.65	-115.8	254.75	-138.95	-341.08
Cam inb gp1 17	86.6	-27.92	-58.68	253.52	158.46	-166.89	8.43	259.45
9848	130.24	-411.97	281.73	-436.20*	27.2	-307.46	280.26	-329.05
CLA 18	155.1	-68.81	-86.29	208.75	213.51	678.56	-892.06*	217.99
ATP S9 30 Y-1	280.4	155.38	-435.78	436.48*	634.38	-89.83	-544.55	-431.89
ATP S5 31 Y-2	20.8	-130.12	109.33	106.39	173.48	-388.74	215.25	308.32
KU1414	313.07	-272.61	-40.46	-123.14	-111.2	-58.53	169.73	274.74
5057	30.32	-98.44	68.13	-334.54	-536.08	394.34	141.74	-235.7
ATP S6 20 Y-2	-507.06	679.45*	-172.39	185.23	-795.1*	339.79	455.31	-84.51
ATP S8 30 Y-3	-187.49	-6.86	194.36	-62.55	20.04	-9.05	-10.99	185.93
CLWN201	275.45	-202.25	-73.2	483.80**	-221.98	143.04	78.94	720.74**
TZMI 102	-355.56	344.13	11.44	-88.74	144.77	-11.23	-133.54	-240.31
J16-1	-115.2	303.93	-188.73	326.14	-337.17	332.91	4.26	728.75**
CLYN246	503.41	-456.75	-46.67	300.65	278.32	-232.95	-45.37	982.75**
CML395	-480.61	229.27	251.34	-283.85	-888.88*	621.06	267.82	125.17
CML494	-198.48	-427.93	626.403*	-299.82	45	-808.92*	763.92	-16.75
CML165	518.95	-355.12	-163.83	-46.53	212.11	-43.25	-168.86	-59.51
CLQRCWQ26	-109.46	159.52	-50.06	396.45*	-290.71	409.14	-118.43	640.10**
CML451	187.95	-374.18	186.23	85.04	548.87	-497.01	-51.85	19.49
V-351-1/6	-31.49	-43.26	74.75	-165.15	-285.87	-229.37	515.24	-557.39*
V-481-73	-594.49	602.76	-8.27	-293.94	-263.1	309.21	-46.11	-751.85**
TZ-STR-133	-272.85	120.64	152.21	121.22	893.04*	-624.02	-269.02	339.57
TL-11-A-1642-5	51.38	648.395*	-699.77*	326.73	752.27	-176.46	-575.81	675.86**
Ku1409	28.66	-16.79	-11.86	15.45	235.94	-392.6	156.66	-26.32
ATP S6-20-Y-1	-98.84	65.49	33.35	504.46**	66.98	207.6	-274.58	538.19*
CML343	-23.52	-75.23	98.76	522.26**	1.66	-516.69	515.03	402.9
CML 444	165.75	468.08	-633.83*	11.67	-140.04	367.64	-227.6	-250.34
4001STR	408.16	-645.52*	237.37	75.15	234.29	-1221.11*	986.82*	190.86
GCA Testers	**72.19**	**59.95**	**-132.13****		**262.49****	**21.36****	**-283.84****	

Note. *, **, Significant at 0.05 and 0.01 probability levels, respectively, and ns, not significant; SCA: Specific combining ability.

4. Discussion

The results of this study revealed that six hybrids yielded more than 3500 kg.ha^{-1} under low N condition. These include TL-11-A-1642-5 × Exp1 24, CLWN201 × 87036, ATP S6 20 Y-2 × Exp1 24, J16-1 × Exp1 24, ATP S9

30 Y-1 × Exp1 24 and CLYN246 × 87036. The best hybrid among the four checks evaluated was 87036 × Exp1 24, and the performance of this hybrid under low N was similar to that obtained (3 t ha^{-1}) by The et al. (2013). Under low N, significant differences were observed among the hybrids for all traits, indicating the variable reaction of the tested genotypes to low N stress. Similar results were obtained by Ifie et al. (2014) under low N. The use of inbred lines from diverse sources of germplasm for generation of the crosses might have contributed to the significant difference observed among crosses for most of the traits considered. Under high N environments, the five highest yielding hybrids were TL-11-A-1642-5 × 87036, CLYN246 × 87036, TZ-STR-133 × 87036, CLWN201 × Exp1 24, and J16-1 × Exp1 24. Each yielded more than 6000 kg ha^{-1}. Under both low and high N environments, the best yielding hybrids out-yielded the four checks among which is the commercial hybrid (87036 × Exp1 24) for the Humid Forest Zone of Cameroon. These could be candidates for release.

In this study, six hybrids were selected from the 20 best hybrids under both low N, high N and across environments. These included CLYN246 × 87036, CLWN201 × Exp1 24, J16-1 × Exp1 24, 1368 × 87036, ATP S6-20-Y-1 × Exp1 24 and Cam inb gp1 17 × 87036. They appear to be 10% better than the best check. Exp1 24 appears to be an excellent line and could be used as a tester for source populations between TL-11-A-1642-5, ATP S6 20 Y-2, J16-1, and ATP S9 30 Y-1. CLWN201 and CLYN246 could be recombined to form a source population with 87036 as the tester.

Under low N, high N and across environments, the majority of hybrids selected for high grain yield had one CIMMYT line and one line developed by the Cameroon national breeding program as parental lines. This suggests that these introduced lines from CIMMYT and those from IRAD are genetically diverse. This result is in agreement with the statement that the development of adapted high yielding hybrids requires that the varieties used as parents are genetically divergent as highlighted in Acquaah (2007).

GCA effects are associated with additive gene effect while SCA effects are associated with non-additive gene action. The results obtained under low N showed that mean squares of both GCA and SCA were significant for all traits except leaf senescence and plant height. This suggests that, except for these two traits, all other traits were controlled by both additive and non-additive gene effects. Furthermore, non-additive gene effect was predominant in the control of grain yield, anthesis-silking interval, leaf chlorophyll content and ear aspect while days to silking, leaf senescence and plant height were influenced mainly by additive gene effects. Similar results on grain yield were earlier reported by Betràn et al. (2003), Gama et al. (2002), Mosisa et al. (2008), Makumbi et al. (2011), Meseka et al. (2006, 2013), and Ndhlela (2012). However, these results are contradictory to those of Below et al. (1997), Kling et al. (1997), Badu-Apraku et al. (2011, 2013), Ifie et al. (2014) and Tamilarasi et al. (2010) who reported predominance of additive gene effects compared to non-additive gene effects for grain yield under low N. The contradictory results might be due to the difference in environments (N stress level) under which the genotypes were tested or genotypic differences among sets of genotypes included in the studies as suggested by Mosisa et al. (2008). This might also be due to the difficulties that statistical models have in predicting non-additive gene effects. The predominance of non-additive genetic effects for grain yield and other traits observed in this set of inbred lines suggests that hybrid development could be employed under low N in order to exploit non-additive gene effect which is based on over dominance and epistasis, being more predictive of heterotic potential.

It was also found that under high N environments, grain yield, days to silking, leaf area and ear aspect were controlled by both additive and non-additive gene effects. Additive gene effect was predominant in the control of all traits except anthesis-silking interval. The higher magnitude of additive gene effects under high N is consistent with the findings of Below et al. (1997), De Souza et al. (2008) and Makumbi et al. (2011). The significant GCA x environment interaction for grain yield and other traits indicates that GCA effects associated with the lines and testers were not consistent over environments.

Lines with best GCA for grain yield under low N were CML 343, ATP S6 20-Y1, CLWN201 1368, ATP S9 30 Y-1 and CLQRCWQ26. The good general combining ability under low N of CLWN201 and CLQRCWQ26 from CIMMYT are in agreement with the description given by CIMMYT (2014). CML343, another line from CIMMYT, was also identified by Makumbi et al. (2011) as a good general combiner for grain yield across all environments in a study of combining ability under low N, drought and well-watered environments. Three lines in this study were also the best general combiners under high N conditions; these are CLWN201, 1368 and CLQRCWQ26. Cla 17 was the best general combiner for days to silking under low N and high N conditions, whereas 5012 was best combiner in both environments for plant height. The best combiners for shorter anthesiilking interval were Cla 17 under low N and ATPS6 20 Y-1 under high N environments. A shorter anthesis-silking interval under low N may imply that the varieties are able to synchronise pollen shedding with silk emergence (Ndhlela, 2012). A reduced anthesis-silking interval is a sign of improved partitioning of assimilates to ears around flowering time (Edmeades et al., 1993). The best combiners for larger leaf area were CLQRCWQ26 under low N and CML343 under high N environments. A larger leaf area could imply a better interception of light by the plant for photosynthesis. These lines identified as best combiners could be used as parents in a breeding program to improve the respective traits as suggested by Girma et al. (2015).

Testers 87036 and Exp1 24 are good general combiners compared to 9071 for grain yield and other traits except for days to anthesis and days to silking. This suggests that under low N, 87036 and Exp1 24 are more capable of contributing alleles for improvement of these traits to hybrids.

4. Conclusions

The results of this study suggest that there is genetic variability among the hybrids evaluated, making it possible to identify desirable hybrids for grain yield and other agronomic traits under low Nitrogen (N) conditions. Many hybrids out-yielded 87036 × Exp1 24 (commercial hybrid used as check) in the study. Among these, three hybrids (CLWN201 × Exp1 24, J16-1 × Exp1 24, and 1368 × 87036) were identified as higher yielding than the best check under low N, high N and across environments and are candidates for release. For specific areas with low N stress or for farmers who cannot afford N fertilizer, TL-11-A-1642-5 × Exp1 24, CLWN201 × 87036 and J16-1 × Exp1 24 may be candidates for release as low N tolerant hybrids. Moreoevr, TL-11-A-1642-5 × 87036, TZ-STR-133 × 87036, CLWN201 × Exp1 24 and J16-1 × Exp1 24 could be proposed for high N conditions after undergoing additional evaluations.

Under low N and high N environments, grain yield and most traits were controlled by both additive and non-additive gene effects with predominance of non-additive gene effect under low N and additive gene effect under high N conditions. Good hybrid development could be achieved under low N through exploitation of this non-additive gene effect, predictive of heterosis. Due to the influence of non-additive gene effect, SCA of crosses could be used together with means for grain yield to classify inbred lines into heterotic groups. In this study, the best general combiners found for grain yield under both low and high N conditions could be used as parents in a breeding program to develop high yielding hybrids for low and high N environments. In each of these environments, the parents identified for good SCA could effectively be included in hybrid breeding programs for the improvement of grain yield.

In conclusion, the better performing testcrosses, inbred lines with desirable GCA and cross combinations with desirable SCA effects for grain yield and other agronomic traits identified under low and/or high N conditions could constitute a source of valuable genetic material for use in future breeding work.

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