Genetic and heritability studies of grain yield and other agronomic traits in low-N maize

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ABSTRACT

A research was conducted at the Biological Garden of Elizade University, Ilara-Mokin, Nigeria to investigate gene actions and heritability estimates for grain yield and other agronomic traits in low-N maize using North Carolina Mating Design III. Two maize inbred lines were crossed to get F_1 and proceed to F_2. Four randomly selected F_2 segregants that serve as male were backcrossed with each of the two parents inbred lines (P_1 and P_2) that serve as female. The crosses generated were evaluated using a randomized complete block design with three replications in the late cropping seasons in 2019 and early cropping season in 2020 under two environments (low and high nitrogen conditions). General combining ability of females was significant for all study traits at $P < 0.05$ while general combining ability of males was significant for all study traits at different probability levels. Specific combining ability was significant for the traits studied ($P < 0.05$) except leaf blight. The environment was also significant for all traits at $P < 0.05$ excepted ear rot that was significant at $P < 0.01$. There was a preponderance of dominance genetic variance for ear height, days to 50% silking, and grain yield while additive genetic variance prevailed over other traits. However, the average dominance ratio was lesser than unity in most of the traits studied. The narrow-sense heritability estimates for study traits ranged from 1.25–79.08%. The results revealed that the additive and dominant gene actions were both important for agronomic traits in low-N maize. Hence, the adoption of reciprocal recurrent selection becomes necessary in incorporating low-N traits into selected elite maize cultivars.

Keywords: Gene actions, grain yield, low-N maize, Nigeria, North Carolina Design III

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INTRODUCTION

Maize (*Zea mays* L.) is a major cereal crop cultivated in Sub-Sahara Africa. It is ranked as the third most important grown cereal crop after wheat and rice globally (Ogunboye *et al.,* 2020*)*. In Sub-Sahara Africa, Badu-Apraku *et al*. (2012) reported that almost 15% of the total calorie intake is from maize grain. Maize cultivation is preferred among farmers due to its high grain yielding potential, early maturity, ease of cultivation, processing, storage, and marketability, varied cultivars available, tolerance to a wide range of pests, insects and weeds infestation, and diseases infection, lesser cost of production compared to other cereal crops such sorghum, rice, wheat, and millet in Sub-Sahara Africa (Jaliya *et al*., 2008; Badu-Apraku, 2010). The gap in maize grain production to its demand in Nigeria is wide

(Adeosun *et al.,* 2019) which leads to an increase in the price of the commodity due to competition among the buyers. Maize productivity per unit land area is lower in the tropical region compared to the temperate region for some reasons such as unstable weather conditions, poor seeds quality, poor soil fertility mainly low soil nitrogen, and poor agronomic management practices among others (Afolabi *et al*., 2019).

Nitrogen deficiency in the soil is one of the most limiting soil nutrients that considerably limit maize growth and development, thus grain yield reduces (Martins *et al*., 2008) and most soils in the tropics are naturally low in nitrogen content (Salami and Agbowuro, 2016). The tropical region is characterized by high rainfall in terms of duration and intensity which resulted in the leaching of soil nutrients and low organic matter in the soil (Carsky and Iwuafor, 1995). Moreover, nitrogen is rapidly lost in the soil through plant uptake, bush burning, and volatilization. Maize is a heavy nutrient feeder plant that requires a high quantity of nutrients particularly nitrogen to boost its growth and productivity (Ogunboye *et al*., 2020).

Nitrogen plays a vital role in crop growth and development (Jat *et al*., 2013). It is a key component of chlorophyll, protein, and amino acids in the plant. It was reported by Wolfe *et al*. (1988) that nitrogen deficiency in the soil might result in 50% losses in maize grain yield in Sub-Sahara Africa. Most of the maize cultivars that are readily available for maize growers in Nigeria require high nitrogen dosage to yield optimally particularly the hybrids or improved cultivars. Cultivation of improved or hybrid maize cultivars in a low-N environment will not yield optimally. The application of nitrogen fertilizer to supplement the available nitrogen in the soil has been a major practice used by the majority of maize growers to boost grain yield (Agbowuro and Salami, 2015). Continuous use of nitrogen fertilizer will not only increase the cost of maize production but has negative impacts on the ecosystem (Tilman *et al*., 2002). However, nitrogen fertilizer is expensive and scarce, and not readily affordable to the poor resource farmers who are the major maize growers in Sub-Sahara Africa.

Nitrogen use efficiency is a complex trait in plants that depends on both genetic and environmental factors and their interactions (Li *et al*., 2015). The development of maize cultivars that are tolerant to low-N conditions and produce optimally will not only reduce the cost of maize grain production. It will ensure food security and sustainability, and also put an end to the havoc done to the environment by the continuous application of nitrogen fertilizer to the soil. Kant *et al.* (2011) reported that a 1% increase in nitrogen use efficiency in crops could save about US$ 1.1 billion yearly. Several researchers had reported that maize exhibits some useful genetic potential that could be used in making improvements for nitrogen use efficiency (Sunday *et al*., 2020). The use of an appropriate breeding method will determine the level of success in developing the desired trait in a plant and the mode of genetic action exhibited by the desired trait will determine the breeding method to adopt. Hybridization as a breeding method is suitable whenever the trait of interest is governed by non-additive gene action, selection is suitable when the desired trait is governed by additive gene action. Recurrent reciprocal selection is an appropriate breeding method to use when both additive and non-additive gene action becomes important in various plant agronomic traits that contributed to the exhibition of the desired trait.

The combining ability of an inbred line depends on its capability to give superior hybrids when crossed with another inbred line. The mean performance of crop genotype in a hybrid combination is termed general combining ability (GCA). Whenever the combinations of accessions in hybrid perform better or worse than what is expected on an average is called specific combining ability (SCA). The significance of GCA is associated with additive genetic effects which are linked with the parental breeding values (Falconer and Mackay, 1996) while SCA is associated with non-additive genetic effects such as dominance, genotype × environment interaction effects, and epistasis (Bello and Olaoye, 2009). The GCA to SCA ratio dictates the dominance of either additive or non-additive genetic action for the traits of interest

(Gama *et al*., 1995). Narrow-sense heritability is described as the expression of the reliability in which phenotypic value assists plant breeder(s) during a breeding program. A good understanding, knowledge, and information on genetic actions for any trait(s), assessment of its additive and non-additive action, as well as its narrow-sense heritability coupled with the degree of dominance ratio cannot be ruled out in deciding the appropriate breeding technique to adopt by plant breeder(s) for improvement to be on made on such trait(s). This work aimed to estimate the additive and non-additive variances, average degree of dominance, and narrow-sense heritability of some genetic parameters for grain yield and other agronomic traits in low-N maize to identify a suitable breeding method to adopt in improving low-N trait in maize.

MATERIALS AND METHODS

Study Area Description and Soil Testing

The research was conducted at the Biological Garden of Elizade University, Ilara-Mokin, Ondo State, Nigeria in the 2019 late cropping season and the 2020 early cropping season. The research site is located within a tropical humid climate on latitude 07.22°N and longitude 05.10°E. The experimental area was 100 m^2 for each cropping season. A composite soil sample of the experimental sites in the two cropping seasons was taken randomly with soil augers at the depth of 0–30 cm before land preparation into a polythene bag and properly labeled. The soil sample was analyzed at the Soil and Land Resources Management Laboratory of Ekiti State University, Ado-Ekiti. This research was conducted under two nitrogen environments as induced by the application of urea fertilizer at the rate of 30 and 90 kg N ha^{-1}.

Experimental Materials and Design and Mating Design

The genetic parent materials used in this experiment comprised two low-N inbred lines (LNTP-YG and TZPBProlC4) obtained from the International Institute of Tropical Agriculture, Ibadan, Oyo State, Nigeria. Homozygosity among the two-parent inbred lines was obtained by selfing the inbred lines five times before crossing was made. The two-parent inbred lines were crossed to get the first filial generation (F_1) and proceed to the second filial generation (F_2). The research materials were produced by backcrossing four randomly selected F_2 segregants which serve as male to each of the two parents (P_1 and P_2) that serve as female according to Hallauer *et al*. (2010). Before crosses were made, ear shoot bags were used to cover the ear shoots immediately after their emergence before silks emerge to avoid any form of pollen contamination. The pollen grains of the predetermined male maize plants were artificially used to pollinate the predetermined female maize plants. Pollen bags were used to cover the pollinated silks immediately after hand pollination to avoid pollen contamination. The pollen bags were properly labeled with permanent ink to avoid mixed up and for proper identification. The crosses generated were evaluated using a randomized complete block design with three replications in the late cropping season in 2019 and early cropping season in 2020.

Cultural Practices

The experimental sites were manually slashed with a cutlass, cleared, and ridged with hoes. The seeds were planted at the depth of 2–3 cm adopting 25 by 75 cm spacing. Two seeds were planted per hill. At eight days after germination, the seedlings were thinned to one per stand. Weeding was carried out manually at 3, 6, 9, 12, and 14 weeks after planting respectively to keep the field free of weeds.

Data Collection and Analysis

Data were collected on plant height (cm), ear height (cm), days to 50% anthesis (day), days to 50% silking (day), anthesis-silking interval (day), weight of 100 seeds (g), stay green, leaf spot, leaf blight, ear rot and grain yield (t ha^{-1}). Fifty maize plants were randomly selected from each plot. The selected plants were tagged to avoid mix-up for continuous data collection. Stay green, leaf spot, leaf blight, and ear rot were rated based on a scale of 1 to 5. The analysis of variance and expected mean square were estimated using the general linear model (GLM) procedure of SAS Institute software (SAS, 1995). The variance components (additive and dominance), narrow-sense heritability, and degree of dominance ratio were computed as described by Sharma (2006) for the crosses for grain yield and other agronomic traits.

RESULTS AND DISCUSSION

Soil Analysis

Table 1 presents the physiochemical properties of the research sites at the depth of 0–30 cm used for the evaluation. The soil analysis indicated that the soil textural class was sandy loam for the two locations. The soil pH was 5.10 and 5.16 for the 2019 and 2020 experimental sites, respectively. The pH of the research sites was still within the range based on the critical pH of 5.0 for the maize plant (Aune and Lal, 1997). The soil nitrogen was presented in percentage. The soil test result revealed that soil nitrogen was deficient at the two research sites, the nitrogen levels were 1.00% for 2019 and 0.91% for 2020, when compared with the critical value of 1.5 g N kg^{-1} for the maize plant (Sobulo and Osiname, 1981). The exchangeable potassium (K^+) was 0.40 and 0.52 cmol kg^{-1} for 2019 and 2020 experimental sites respectively which were lesser than the critical range of 0.6–0.8 cmol kg^{-1}. The available phosphorus in 2019 (8.50 mg kg^{-1}) and 2020 (9.02 mg kg^{-1}) experimental sites was far below the critical range of 10–15 mg kg^{-1} (Agboola and Corey, 1973).

Table 1 Physiochemical properties of the soils in the experimental sites

Soil properties	Experimental sites	
	2019	2020
Sand (%)	68.00	65.00
Clay (%)	17.00	19.00
Silt (%)	15.00	16.00
Textural class	Sandy loam	Sandy loam
pH	5.10	5.16
Carbon (%)	0.78	0.82
Organic matter (%)	1.26	1.34
Nitrogen (%)	1.00	0.91
Phosphorus (mg kg^{-1})	8.50	9.02
K^+ (cmol kg^{-1})	0.40	0.52
Mg^{2+} (cmol kg^{-1})	0.52	0.56

Mean Performance

The analysis of variance for all study traits is shown in Table 2. Understanding the mode of inheritance in any agronomic trait in plants with the help of GCA and SCA will guide plant breeder(s) in selecting the most effective breeding techniques to adopt when improving on the trait (Derera *et al.*, 2008). The GCA of females was significant for all traits ($P < 0.05$). Likewise, the GCA of males was also significant for all traits although at different probability levels. Plant height, ear height, days to 50% silking, weight of 100 seeds, stay green, and grain yield were significantly affected by GCA of males at $P < 0.05$ while other traits were significantly affected at $P < 0.01$. Moreover, the SCA was significant for all traits except for leaf blight. The significance of GCA and SCA among the traits indicated that both additive and non-additive gene actions played an active role in the inheritance of the traits. These results are in agreement with the findings of Salami and

Agbowuro (2016) who reported the significances of both additive and non-additive gene actions in maize grain yield and related traits. They recommended that the adoption of reciprocal recurrent selection breeding method is an effective method in improving maize grain and related traits in stressed and non-stress low-N soil conditions. Although, the results contradicted the findings of Sunday *et al*. (2020) who reported that additive gene action is mainly involved in determining the grain yield and associated traits in maize, hence selection breeding method is appropriate in improving maize grain.

The environment was also significant for all traits at $P < 0.05$ except for ear rot that was significant at $P < 0.01$. This result implied that environmental variables can be altered to get the desired breeding target in a tested environment for all traits. Moreover, the instability of the study traits was obvious across the various environments. The interactions between GCA and SCA and environment were significant for some traits (Table 2). The results indicated that both additive and non-additive gene actions are important in the expression of these agronomic traits. The high level of significance in the result showed the existence of a high level of genetic variability to be exploited in crop improvement that shown a broad range observed for each trait. The findings of this research are in agreement with the results of Oikeh (1996), Keimeso and Abakemal (2020) and Sunday *et al*. (2020) who reported a high level of significance among study traits in low-N maize.

Gene Actions

Variance components

The estimated variance components of the agronomic traits are presented in Table 3. Large variation was observed for all components with additive genetic variance ranging from 0.004 for leaf blight to 185.788 g^2 for weight of 100 seeds and dominance genetic variance ranges from –0.080 day^2 for anthesis-silking interval to 483.248 cm^2 for ear height. While the degree of dominance ratio and average degree of dominance ranged from –0.50 for leaf blight to 78.61 for ear height and –0.57 for leaf blight to 145.23 for days to 50% silking, respectively. The magnitude of dominance genetic variance was less than the additive genetic variance for study traits excepted ear height, days to 50% silking, and grain yield. The results revealed that there was a preponderance of additive genetic variance for plant height, days to 50% anthesis, anthesis-silking interval, weight of 100 seeds, stay green, leaf spot, leaf blight, and ear rot, and these traits could be governed by additive genes that are related to homozygosity and are fixable. There was also a preponderance of dominance genetic variance for ear height, days to 50% silking, and grain yield which was controlled by non-additive genes. Trait(s) that are governed by non-additive gene action understudy could be improved through heterosis breeding while those controlled by additive gene action could be improved through selection (Mahalingam *et al*., 2011).

The average dominance ratio determines the average level of dominance (Sharma, 2006). The average degree of dominance action equal to zero indicated the absence of dominance genetic action. In the case where the average dominance ratio is equal to one, lesser than one, or greater than one means there is a complete dominance action, partial dominance action, or overdominance action, respectively (Elia *et al*., 1997; Salami and Agbowuro, 2016). This result revealed that the average degree of dominance ratio was greater than one for ear height, days to 50% anthesis, days to 50% silking, and grain yield which indicated overdominance gene action. Other traits except for anthesis-silking interval and leaf blight showed an average degree of dominance greater than zero but less than one which indicated a partial dominance for these traits. The traits exhibited an average degree of dominance ratio greater than zero indicated that these traits could be governed by the dominance genes and hybridization could be an appropriate breeding method to adopt for their improvement. The average degree of dominance ratios for anthesis-silking interval and leaf blight were zero which indicated the absence of dominance gene action. Hence, these two traits were controlled by additive genes. Therefore, selection as a breeding strategy should be adopted for improving these traits.

Table 2 Mean squares from analysis of variance for grain yield and other selected agronomic traits

Traits	Replication	F	M	F × M	ENV	F × ENV	M × ENV	F × M × ENV	Error
df	2	1	3	3	3	3	9	9	70
PH	557.841	106.207*	140.762*	31.124*	281.306*	4.561**	3.724**	1.850	7.987
EH	86.153	179.413*	11.610*	727.264*	33.660*	0.043	0.094	0.719	2.390
ANT50%	13.270	121.603*	1.568**	1.587**	18.253*	0.013	0.748*	3.689*	0.505
SILK50%	12.750	89.920*	1.213*	1.680**	10.923*	0.013	0.472*	3.447*	0.598
ASI	0.003	0.820*	0.179**	0.068*	0.634*	0.137*	0.100*	0.196**	0.189
SW100	421.600	296.018*	386.256*	90.946*	254.844*	6.303*	0.640	0.814	8.316
SG	1.341	0.889*	0.174*	0.600*	8.701*	0.134	0.033**	0.010	0.074
LS	0.134	0.089*	0.206**	0.203**	3.040*	0.520*	1.520**	0.006**	0.164
LB	0.398	0.042*	0.100**	0.089	1.886*	0.005**	0.086**	0.104**	0.093
ER	0.145	0.189*	0.156**	0.095**	0.006**	0.187*	0.046**	0.281*	0.075
GY	0.261	1.204*	0.045*	0.259*	1.927*	0.001*	0.011*	0.022*	0.004

Note: *, ** Significant at 0.05 and 0.01 levels of probability, respectively

F = general combining ability of females, M = general combining ability of males, F×M = specific combining ability, ENV = environment, df = degree of freedom, PH = plant height (cm), EH = ear height (cm), ANT50% = days to 50% anthesis (day), SILK50% = days to 50% silking (day), ASI = anthesis-silking interval (day), SW100 = weight of 100 seeds (g), SG = stay green, LS = leaf spot, LB = leaf blight, ER = ear rot, GY = grain yield (t ha^{-1})

Table 3 Variance components, degree of dominance ratio, and heritability estimates for agronomic traits

Traits	**δ^2A**	**δ^2D**	**DD**	**h^2 (%)**
PH	88.516 ± 16.939	15.424 ± 10.704	0.174	79.08
EH	6.144 ± 9.234	483.248 ± 42.840	78.653	1.25
ANT50%	0.668 ± 13.865	0.662 ± 0.548	1.021	35.70
SILK50%	0.408 ± 10.525	0.720 ± 0.088	1.764	23.64
ASI	0.628 ± 0.094	–0.080 ± 0.420	0	85.21
SW100	185.788 ± 39.077	55.086 ± 30.424	0.296	74.56
SG	0.064 ± 0.101	0.035 ± 0.196	0.546	36.99
LS	0.028 ± 0.014	0.026 ± 0.064	0.002	12.84
LB	0.004 ± 0.006	–0.002 ± 0.060	0	4.21
ER	0.052 ± 0.022	0.012 ± 0.028	0.230	37.41
GY	0.024 ± 0.015	0.170 ± 0.084	7.083	12.12

Note: Values of δ^2A and δ^2D are presented as estimates ± standard error with unit^2
δ^2A = additive genetic variance, δ^2D = dominance genetic variance, DD = degree of dominance ratio, h^2 = narrow-sense heritability, PH = plant height (cm), EH = ear height (cm), ANT50% = days to 50% anthesis (day), SILK50% = days to 50% silking (day), ASI = anthesis-silking interval (day), SW100 = weight of 100 seeds (g), SG = stay green, LS = leaf spot, LB = leaf blight, ER = ear rot, GY = grain yield (t ha^{-1})

Heritability

Heritability is a degree to which the genotype of an individual determines its phenotypic expression, it gave insight into how a trait could be effectively transmitted from one generation to another (Burton, 1952; Hallauer *et al*., 2010). Narrow-sense heritability is the manifestation of the reliability in which phenotypic value assists in the breeding value. Robinson *et al*. (1955) classified heritability percentage as below 30% for low, 30–60% for moderate, and above 60% for high. Low heritability percentage in a narrow-sense shows that the trait is governed by a non-additive gene while high narrow-sense heritability shows that the trait is governed by an additive gene (Ansari *et al*., 2004). High heritability shows a large heritable variance that could likely improve crop through selection (Acquaah, 2012). Likewise, heterosis breeding (hybridization) is a breeding technique to adopt when making crop improvements whenever the heritability percentage is low. Sardana *et al*. (2007) explained that high heritability percentage is not the only factor that leads to increased genetic gain, sufficient genetic variability among the germplasm is another key player when considering genetic gain increment. In this research, the narrow-sense heritability estimates were moderate to high (greater than 30%) for plant height (79.08%), anthesis-silking interval (85.21%), weight of 100 seeds (74.56%), days to 50% anthesis (35.70%), stay green (36.99%), and ear rot (37.41%) while other agronomic traits, heritability estimates were below 30% including grain yield (12.12%). Considering grain yield, the most valuable and economic part of maize, the result showed higher non-additive genetic values over additive genetic values (Table 3). The average dominance ratio for grain yield was greater than one which reflected that non-additive gene action was in control. Moreover, based on the heritability classification of Robinson *et al*. (1955), the narrow-sense heritability estimate for grain yield was low that showed a greater proportion of non-additive genetic variation. Estimated narrow-sense heritability also indicated that grain yield was governed by a non-additive gene. Whereas plant height, days to 50% anthesis, anthesis-silking interval, weight of 100 seeds, stay green and ear rot were governed by additive gene action.

These results are in disagreement with the findings of Rizzi *et al.* (1993) and Below *et al.* (1997) who reported that selection as a breeding strategy should be adopted in developing low-N traits in maize cultivar and Kasantonis *et al.* (1988) who reported that hybridization as a breeding method should be adopted in developing low-N trait. The results are in agreement with Betran *et al.* (2013) who reported that both additive and non-additive gene actions were responsible for yield under low nitrogen conditions. The disagreement could be as a result of different environments that the experiment was conducted, and the genetic make-up of the inbred lines used (Li *et al*., 2015).

CONCLUSIONS

The study revealed the preponderance of both additive and non-additive genetic actions for agronomic traits in low-N maize. Improvement of any trait(s) relies on the gene(s) controlling the trait(s) and the kind of genetic action(s) involves in determining the type of breeding method to adopt. The existence of both additive and non-additive variance is a prerequisite through reciprocal recurrent selection. Hence, it is recommended that the use of reciprocal recurrent selection should be adopted by plant breeders for developing low-N maize in the rainforest agro-ecological zones of Nigeria.

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