Gene action in low nitrogen tolerance and implication on maize grain yield and associated traits of some tropical maize populations

Abstract: Understanding the mode of inheritance of traits is vital in the selection of breeding methods for the grain yield and improvement of associated traits in a target environment. Combining ability is one of the powerful indices for the selection of the best cross combinations, parental lines that combine with other lines and the best breeding method for high grain yield improvement programmes. A total of 45 crosses were generated from ten maize varieties developed in low nitrogen environment in a diallel mating fashion without reciprocal. The resultant progenies were investigated in low- and high-nitrogen soil to identify the mode of grain yield inheritance and those of related traits in the tested environments. Mean square analysis revealed the preponderance of additive and non-additive gene actions in the expression of maize grain yield and related characters tested under stress and optimal conditions. In this study, it is proved that both standard selection and hybridization breeding strategies are effective for the improvement of most traits involved. This experiment also confirmed the adequacy of sufficient variation in the gene pool present in the maize population that could be exploited in maize grain yield improvement programmes in the tropics. The ratio of SCA to GCA however emphasized the superiority of additive gene effects in the expression of most traits in the tested environments. The results, therefore, suggest that additive gene actions primarily condition the expression of maize grain yield and associated characters in the tested environments. Therefore, suggesting that the standard selection method would be effective for the improvement of most traits tested under the two environments.

Keywords: gene action, GCA and SCA, additive, non-additive, maize

1 Introduction

Proper selection of parental lines for the generation of high-yielding inbred lines is highly essential in maize hybrid development programmes. However, identification of appropriate breeding methods for the improvement of the target traits is equally significantly important in maize improvement programmes. Understanding the mode of gene action that conditions the expression of a target trait to be improved determines (Tilman et al. 2002) the type of breeding methods that can be exploiting for the development of high grain yield and other yield-related components (Bocanski et al. 2010). Hybridization method is appropriate for a target trait that is controlled by non-additive type of gene action, while a standard selection method is required for a trait that is controlled by additive type of gene action. Analysis of combining ability is the appropriate method for the identification of gene action that conditions various crop traits to be improved. The ratio of GCA to SCA determines the preponderance of either additive or non-additive gene action over one another for the target traits (Gama et al. 1995; Beck et al. 1990). When GCA/SCA is >1 for a trait, it suggests the preponderance of additive gene action effects over the non-additive one, and thus the selection method is appropriate for the improvement of such traits. However, when the ratio of GCA to SCA <1, it suggests that the traits were highly influenced by non-additive genetic effects. Hence, hybridization is the best breeding method for improving such traits. Derera (2007) conducted an experiment to investigate the mode of inheritance of maize grain yield and associated characters using North Carolina design II methods to generate 72 progenies from 27 inbred
lines. The author evaluated both the 72 genotypes and eight commercial hybrids in four drought and two non-drought environments by exploiting the $8 \times 10$ α-lattice design with two replications. The result of the study revealed that only the GCA effect was significant for maize grain yield, indicating the high influence of additive gene action effects on the expression of the trait. However, in humid environments, both GCA and SCA were significant for the expression of grain yield, indicating that both additive and non-additive gene actions influence the expression of grain yield in tested environment, respectively, which suggested that either the selection or hybridization breeding strategy could be exploited for the improvement of maize grain yield in the rain forest zone or optimum water availability environment. Also, Salami and Agbowuro (2016) investigated the mode of inheritance of maize grain yield and disease incidence coupled with the estimation of heritability percentage of low nitrogen (low N) maize materials. They reported the preponderance of dominance genetic variance for ear and plant aspect and leaf spot. The study also revealed high influence of additive gene action effects on maize grain yield. Therefore, they suggested that the use of reciprocal recurrent selection is a better method for incorporating the gene that conditions the target character into the elite maize varieties under low-N condition. In another view, Falconer and Mackay (1996) also reported that the significance of GCA explains the contribution of the breeding value of the parents, which also associates with the additive genetic effects, while SCA implies the presence of non-additive gene effects such as dominance, epistasis and genotype × environment interaction effects (Bello and Olaoye 2009). Jean et al. (2016) also emphasized the importance of understanding the mode of gene action that conditions the expression of desire traits to be improved in a target environment. This knowledge will assist the breeders in identifying suitable parents and crosses for the generation of lines for future breeding activities (Falconer and Mackay 1996). Mondal and Hossain (2006) also agreed that both GCA and SCA help in identifying the best parental lines and hybrids for future international trials. Similar observation was confirmed by Bradshaw and Mackay (1994) and Falconer and Mackay (1996) that GCA indicates the average contribution of a parent to its progeny. However, SCA was observed to provide information on the deviation of the progenies means from that of their parents (Bradshaw and Mackay 1994).

This experiment was conducted to investigate the nature and the magnitude of gene action that conditions the expression of grain yield and associated traits under low-N environment and thereby identify suitable breeding methods that can be exploited when planning strategies for the development of low N maize tolerance in the tropics (Smith et al. 1995).

2 Materials and methods

Ten open-pollinated varieties (OPVs) of maize, which were developed for grain yield and associated characters at the International Institute of Tropical Agriculture, Ibadan, were used for the experiment. A total of 45 F1 hybrids were generated from the ten OPV maize populations, and the resultant progenies were harvested, processed, fumigated and stored in the cold room prior to field evaluation. The 45 F1 crosses and their ten parents were tested in six environments, namely, Ife and Ikenne, regarded as optimal environment; Mokwa (latitude $9^\circ18'N$, longitude $5^\circN4'E$) and Zaria (latitude $12^\circ00'N$, longitude $8^\circ22'E$) (Guinea savanna) where the genetic materials were evaluated under high- and low-N conditions with two different levels of nitrogen application (30 and 90 kg ha$^{-1}$), respectively. Planting space was 75 cm × 25 cm, with two row plots and four replications. Data collected on grain yield and related traits were subjected to analysis of variance (ANOVA). The least significant difference test according to Steel and Torrie (1980) was used to separate the means.

3 Results and discussion

The combined ANOVA for combining ability for grain yield and agronomic traits under natural growing conditions (Ife and Ikenne) revealed that the two environments (E) differed significantly for all traits measured except grain yield, days to 50% anthesis, anthesis–silking interval and ear aspect (Table 1). Genotype (G) mean square effects were only significant for the number of ears per plant, days to 50% silking and plant and ear heights. The GCA and SCA mean square effects were both significant for days to 50% silking, days to 50% anthesis and plant height, respectively, which indicates that both additive and non-additive gene actions are involved in the inheritance of the three traits. According to Salami and Agbowuro (2016), the use of reciprocal recurrent selection procedure can be adopted for the improvement of these traits. That the ratio of GCA to SCA is greater than 1 indicated that the component of the additive gene action is higher than that
of non-additive action in the inheritance of most of the traits tested under optimal environment. Thus, selection methods will be more adequate for the improvement of the most traits under stress-free environment (Edwards et al. 1976). GCA and SCA × environment interaction mean square effects were not significant for any of the traits, indicating the stability of these breeding procedures across different breeding environments. The results also revealed the preponderance of GCA component in the expression of grain yield–related components except plant height, husk cover and ear aspect, suggesting that the selection method will be appropriate for most of the tested traits.

The data in Table 2 reveal that the differences between the two different levels of nitrogen were significant for grain yield, days to 50% anthesis and 50% silking, root and stalk lodging, ear aspect and number of ears per plant. Differences between parental varieties were only significant for days to 50% anthesis and plant and ear heights under low-N and high-N environments. Significant differences were recorded among hybrids for grain yield, anthesis–silking interval, plant height and husk cover. Differences between hybrids and the parental varieties were significant for grain yield, days to 50% anthesis, stalk lodging, plant and ear aspects. Interactions between genotypes and different nitrogen levels were not significant for any traits under consideration.

Results of diallel analysis under low-N and high-N conditions at Mokwa and Zaria showed that environmental (E) effects were highly significant for all measured traits (Tables 3 and 4). The genotypes (G) differed significantly for only grain yield, days to 50% anthesis and

---

### Table 1: ANOVA of combining ability for grain yield and agronomy traits in F1 hybrids and parents across stress-free condition (Ikenne and Ife 2012)

| Source                  | Df | Yield (t/ha) | Ear per plant (no) | Anthesis (days) | Days to silk (days) | Anthesis silking interval (days) | Plant height (cm) | Ear harvest (no) | Husk cover (1–5) | Ear aspect (1–5) |
|-------------------------|----|-------------|--------------------|-----------------|--------------------|----------------------------------|-------------------|-----------------|------------------|-----------------|
| Env                     | 1  | 2237.14     | 1.15**             | 0.82            | 1716.28**          | 0.4                              | 5418.04**         | 1069.54**       | 257.65**         | 1.20            |
| Rep/Env                 | 6  | 2501.97     | 0.59**             | 13.72**         | 7.31**             | 0.5                              | 1534.76           | 207.12**        | 5.95**           | 15.33**         |
| Genotypes               | 54 | 2556.04     | 0.15               | 12.74**         | 7.43**             | 0.25                             | 1100.88*          | 47.52*          | 1.66             | 4.39            |
| GCA                     | 9  | 4708.35     | 0.17               | 34.11**         | 26.26**            | 0.53                             | 768.28            | 74.39*          | 1.56             | 3.42            |
| SCA                     | 45 | 2125.57     | 0.15               | 8.46            | 3.66**             | 0.19                             | 1167.40*          | 42.15           | 1.67             | 4.59            |
| Env × Gen               | 54 | 2553.3      | 0.15               | 6.09            | 1.16               | 0.24                             | 484.58            | 33.91           | 2.22             | 5.16            |
| GCA × Env               | 9  | 4724.83     | 0.15               | 4.12            | 1.34               | 0.37                             | 314.99            | 31.79           | 1.98             | 3.48            |
| SCA × Env               | 45 | 2118.99     | 0.14               | 6.48            | 1.12               | 0.22                             | 518.5             | 34.34           | 2.26             | 5.49            |
| Pool error              | 324| 2571.59     | 0.12               | 6.11            | 1.42               | 0.27                             | 741.11            | 32.21           | 1.98             | 4.76            |
| SCA/GCA                 | 0.45| 0.84        | 0.25               | 0.14            | 0.36               | 1.51                             | 0.57              | 1.0             | 1.0              | 1.0             |

*Significant at <0.05 level of probability. **Significant at <0.01 level of probability.

### Table 2: ANOVA for grain yield and agronomy traits in F1 hybrids and parents under low-N versus high-N at Mokwa and Zaria (2012)

| Sources | DF | Yield (t/ha) | Anthesis (days) | Days to silk (days) | Anthesis silking interval (days) | Plant height (cm) | Ear harvest (no) | Husk cover (1–9) | Plant aspect (1–9) | Ear aspect (1–9) | Ear per plant (no) |
|---------|----|-------------|-----------------|--------------------|----------------------------------|-------------------|-----------------|------------------|-------------------|-----------------|------------------|
| N/level | 1  | 2.95*       | 203.84*         | 69.05*             | 6.06                             | 4387.76           | 500.15          | 2.53             | 0.00              | 180.61          | 11.12*            |
| Rep/N   | 6  | 7.54        | 12.97           | 92.96              | 3.05                             | 34184,20          | 1456.92         | 3.04             | 16.64            | 434.97          | 13.20             |
| Genotype| 54 | 35.41       | 352.98          | 1.19               | 1539000                        | 275.08            | 0.73            | 0.79             | 177.27           | 1.26            | 0.15             |
| Parent (P) | 9 | 0.73        | 18.97*          | 203.73             | 0.56                             | 30543.4*          | 1078**          | 0.73             | 0.33             | 1355.20         | 1.07              |
| Cross (C) | 44| 0.81*       | 35.53           | 139.15             | 0.61**                          | 532.42*           | 269.28          | 0.68*            | 0.70             | 41.29           | 1.35              |
| P × C   | 1  | 36.53**     | 339.72**        | 24.87              | 5.83                             | 2043.95           | 641.09          | 2.28             | 4.91*            | 964.50*         | 9.22*             |
| Gen × N | 54 | 0.44        | 9.27            | 75.59              | 0.01                             | 3361.18           | 318.64          | 0.38             | 0.64             | 137.80          | 1.00              |
| Error   | 324| 1.88        | 32.55           | 87.76              | 0.65                             | 4018.00           | 609.99          | 0.86             | 0.92             | 204.70          | 1.21              |

*Significant at <0.05 level of probability. **Significant at <0.01 level of probability.
silking, husk cover and ear harvest under low-N condition, while G × E interaction effects were not significant for any of the traits. Both GCA and SCA mean square effects were significant for grain yield, days to 50% anthesis and ears harvested. GCA mean square effects were also significant for root lodging under low-N condition. GCA and SCA × environment interaction effects were not significant for any trait. The ratio of GCA to SCA under low-N environment revealed that the component of GCA variance was higher than SCA for most of the traits except ear placement, plant and ear aspects. This suggests the adequacy of standard selection methods for the improvement of those traits under low N environments.

Environmental (E) effects were significant for all the traits measured under high-N conditions (Table 4), which indicates that variable environmental factors can be modified to meet a desirable goal under the tested environment. However, it also suggests the instability of the traits across different environments. Genotypic (G) effect was also significant for grain yield, days to 50% anthesis, anthesis silking interval (ASI), ears at harvest and ear aspect. GCA and SCA mean square effects were significant for days to 50% anthesis and ASI, which indicates that both additive and non-additive gene effects play vital role in determining maize flowering dates. G × E interaction effect was only significant for husk cover, which suggests the influential effects of environment on husk cover aspect under high N condition. GCA × E interaction effect was only significant for husk cover but not for other traits measured under high-N conditions. Thus, a standard selection method will be adequate for the improvement of all the traits tested except husk cover in any environments. The results also revealed that the SCA × E interaction effect was not significant for any of the traits. This signifies that the non-additive gene effect does not play a vital role in the expression of all the tested traits. Similar to low-N environment, the ratio of SCA to GCA that is less than 1 indicates a preponderance of GCA component in the expression of all the traits tested under high-N environment except stalk lodging and ear harvest.

Results of diallel analysis under low-N and high-N conditions at Mokwa and Zaria showed that environmental (E) effects were highly significant for all measured traits (Table 3). The genotypes (G) differed significantly for only grain yield, days to 50% anthesis and silking, husk cover and ear harvest under low-N condition, indicating the availability of adequate variability among the plant populations that can be manipulated for the improvement of those traits (Sharma et al. 2004). However, G × E interaction effects were not significant for any of the traits, suggesting the stability in the expression of those traits if selected, across various environments. In a similar view, Machado et al. (2009) conducted a study and observed lack of significant mean square estimates of SCA × E interaction for some traits tested and therefore suggested that expressions of such traits among the single cross hybrids were consistent across environments and concluded that a good selection progress for improvement of such traits was feasible under any environment as similarly observed by Machado et al. (2009).

Both GCA and SCA mean square effects were significant for grain yield, days to 50% anthesis and ears harvested. GCA mean square effects were also significant for root lodging under low-N condition. GCA and SCA × environment interaction effects were not significant for any trait. The ratio of GCA to SCA under low-N environment indicated that the component of GCA variance was higher than SCA for most of the traits except ear placement, plant and ear aspects.

GCA and SCA are good selection indices for identifying the best parents and crosses that could be used to exploit heterosis or accumulate productive alleles for the desired traits. They are also helpful in understanding the mode of inheritance of many characters that enable the plant breeder design effective breeding strategies for future maize grain yield development programmes (John et al. 2007). The significant GCA and SCA mean squares in this study indicated that both additive and non-additive gene actions were important in the inheritance of the traits under the specific environments in which the studies were conducted. It also confirmed the presence of sufficient genetic variation inherent in the populations that could be exploited for genetic improvement of grain yield and other desirable agronomic traits. However, the ratio of SCA to GCA effects indicated a predominance of additive gene effects in the expression of most traits across the two studied environments (Muhinyuza et al. 2016). This suggested that the recurrent selection method will be effective in the improvement of most of the associated traits across environment conditions.

The significance of GCA and SCA mean squares for anthesis, days to silk, plant height, husk cover and number of harvestable ears per plot indicated relative importance of additive and non-additive gene actions for these traits under low-N condition. Selection protocol, couple with hybridization will therefore be effective for the aforementioned traits. However, the non-significant G × E, GCA × environment and SCA × environment mean square effects for these traits indicated that their
expressions remained stable across the different low-N environments. Furthermore, the significant GCA × environment interaction mean squares observed for ear number per plant across low and high-N levels and for ear height and husk cover under high-N condition indicated that the parental lines exhibited differential performance in hybrid combinations for these traits under different environmental factors in this study. GCA mean squares were significant for days to 50% anthesis and silking as well as ASI. This observation was similar to the results obtained under high-N environment. These revealed the importance of additive gene action for the expression of these traits across abiotic and biotic stress environments.

4 Conclusion

The results, therefore, suggest that additive type of gene action is primarily involved in determining grain yield and related traits across all the tested environments, which indicates that the standard selection method would therefore be effective in improving maize grain yield and related traits in stressed and non-stressed environments, most importantly in the low-N soil conditions that characterize most of the tropic soil.

Conflict of interest: The authors declare no conflict of interest.

References

[1] Beck DI, Vaal SK, Carossa J. Heterosis and combining ability of CIMMYT’s tropical early and intermediate maturity maize (Zea mays L.) germplasm. Maydica. 1990;35:279–85.
[2] Bello OB, Olaoye G. Combining ability for maize grain yield and other agronomic characters in a typical Southern Guinea Savanna ecology of Nigeria. Afr J Biotechnol. 2009;8(11):2518–22.
[3] Bocanski J, Srećkov Z, Nastić A, Ivanović M, Djalović I, Vukoša V. Mode of inheritance and combining abilities for kernel row number, kernel number per row and grain yield in maize (Zea mays L.). Genetika. 2010;42(1):169–76.
[4] Bradshaw JE, Mackay GR. Breeding strategies for clonally propagated potatoes. In: Bradshaw JE, Mackay GR, editors. Potato genetics. Wallingford: CAB International; 1994.
[5] Derera J, Tongonpa P, Vivek B, Laing M. Gene action controlling grain yield and secondary traits in southern African maize hybrids under drought and non-drought environments. Euphytica. 2007;162(3):411–22.
[6] Edwards LH, Ketata H, Smith EL. Gene action of heading date, plant height and other characters in two winter wheat crosses. Crop Sci. 1976;16:275–7.
[7] Falconer DS, Mackay TFC. Introduction to quantitative genetics, 4th edn. Harlow, England: Pearson Prentice Hall; 1996.
[8] Gama EGG, Hallauer AR, Ferrão RG, Barbosa DM. Heterosis in maize single crosses derived from a yellow Tuxpeño variety in Brazil. Brazilian J Genet. 1995;18:81–5.
[9] John D, Tongonpa P, Vivek B, Laing M. Gene action controlling grain yield and secondary traits in southern African maize hybrids under drought and non-drought environments. Euphytica. 2007;162(3):411–22.
[10] Machado JC, de Souza JC, Ramalho MA, Lima JL. Stability of combining ability effects in maize hybrids. Sci Agric. 2009;66:494–8.
[11] Mondal MA, Hossain MM. Combining ability in potato (Solanum tuberosum L.). Bangladesh J Bot. 2006;35:125–31.
[12] Muhinyuza JB, Shimelis H, Melis R, Sibiya J, Nzaramba MN. Combining ability analysis of yield and late blight [Phytophthora infestans (Mont.) de Bary] resistance of potato germplasm in Rwanda. Australia J Crop Sci. 2016;10(6):799–807.
[13] Salami AE, Agbowuro GO. Gene action and heritability estimates of grain yield and disease incidence traits of low-N maize (Zea mays L.) inbred lines. Agric Biol J North Am. 2016;7(2):50–4.
[14] Sharma HC, Sharma KK, Crouch JH. Genetic transformation of crops for insect resistance: potential and limitations. Crit Rev Plant Sci. 2004;23:47–72.
[15] Smith ME, Miles CA, Van Beem J. Genetic improvement of maize for nitrogen use efficiency. In: Jewell DC, Waddington SR, Ransom JK, Pixley KV, editors. Maize research for stress environments. Proceedings of the 4th Eastern and Southern Africa Regional Maize Conference, Harare, Zimbabwe, 28 March–1 April 1994. Mexico: CIMMYT. 1995. p. 306.
[16] Steel RGD, Torrie JH. Principles and procedures of statistics. 2nd edn. New York: McGraw-Hill Book Co; 1980.
[17] Tilman D, Cassman KG, Matson PA, Naylor RL, Polasky S. Agricultural sustainability and intensive production practices. Nature. 2002;418:671–7.