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Gene Action Mechanism for Drought Tolerance in Extra-Early Yellow Maize Inbreds

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ABSTRACT

The effect of drought on crops is very significant and will affect world food supply due to climate change. Gene action, general combining ability (GCA) and specific (SCA) combining ability of 66 single cross hybrids of extra early maize derived using the diallel mating design involving 12 parents were evaluated under drought conditions. The design of the experiment was a 10 × 7 randomised incomplete block design with two replications. The mean squares of GCA were larger than those of SCA for the observed traits except for grain yield. The relative importance of GCA over SCA was observed to be close to unity for some of the observed traits. The correlation between yield and plant aspect, anthesis silking interval, ear aspect and stay green characteristics (SG) was negative and significant. Selection for genotype with low values in these traits will lead to indirect selection for high yielding genotypes. The inbred TZdEEI 11 and a hybrid, TZdEEI 1 × TZEEI 58, which had highly significant positive GCAs for grain yield and negative GCAs for SG, were identified as a good inbred line tester and single cross tester, respectively. From the study, the inheritance of genes was an additive effect, therefore, the prediction of performance of hybrids for the traits observed under drought conditions can be done using only GCA except for grain yield.

Keywords: Diallel, drought, extra early maize, GCA, grain yield, SCA

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INTRODUCTION

Maize (*Zea mays* L.), being a primary staple food crop, provides calories for over 300 million people in West Africa. In Nigeria, the average yield per hectare is about 1.8 ton per ha (FAO Statistics Division, 2014) in the face of the availability of high yielding varieties and better crop management when compared to 9.5 tons per ha in the USA and the world average of 5.5 tons per ha (Adnan et al., 2017). Low grain yield has been mainly attributed to biotic and abiotic stresses. Abiotic stress such as drought is becoming a permanent characteristic of sub-Saharan African climate. It has been reported that drought can reduce grain yield by 53% (Badu-Apraku et al., 2004). This reduction in grain yield has key effects on the world food supply due to the effects of climate change (Edmeades, 2013). In drought-prone areas, extra early maize varieties are highly desirable because of their reduced maturity period compared with other maturity groups. Identifying extra early maize that is drought tolerant will be an added advantage to farmers as the plant will be able to reach physiological maturity before the initiation of drought.

Host plant resistance is an economically feasible method of developing a drought-tolerant genotype but there is a need to identify drought tolerance testers that can be hybridised to exploit heterosis. Selection of lines with good grain yield and drought tolerance will require deciphering the genetic variances (combining ability) present in the genotypes. There are many ways of determining the combining ability of plants including diallel mating design. The diallel mating system allows statistical separation of progeny performance into GCA and SCA. Extra early inbred lines that are drought tolerant have been developed by the International Institute of Tropical Agriculture (IITA). However, only a few extra early maturing maize varieties can tolerate drought. There is, therefore, a need to make crosses among these inbreds and select promising genotypes that will be able to tolerate, avoid and or escape drought. The aim of this research was to evaluate the performance of extra-early yellow maize single cross hybrids to determine gene action and examine their combining ability. Inbreds and hybrid testers tolerant to drought were also identified.

MATERIALS AND METHOD

A diallel mating system using 12 inbreds from the International Institute of Tropical Agriculture (IITA) was used to derive 66 single crosess without their parents and reciprocals. The crosses were generated during the wet season of 2013. The diallel crosses together with four checks were evaluated during the dry seasons of 2013/2014 at Ikenne using a 10 × 7 randomised incomplete-block design with two replications. The crosses were sown in single-row plots of 5 m in length with intra and inter row spacing of 0.4 m and 0.75 m, respectively.

Drought stress was imposed according to the method of Badu-Apraku et al. (2012). Irrigation was done for 21 days after planting (V5 to V6), after which the plants were left without water supply up to harvest. Fertiliser was applied at planting at the rate of 60 kg ha-1 N, P, and 60 kg ha-1 N was used to top dress at 2 weeks after planting (WAP). Data were recorded for days to anthesis: number of days to when

50% of the plant had shed pollen, days to silking, and number of days to when 50% of the silks had emerged, plant and ear height. These were measured in cm as the distance from the base of the plant to base of the tassel and upper cob, respectively. Stay green characteristics and ear aspect were scored using a 1-9 scale based on visual observations with 1 indicating <10% damage and 9 >90% damage. The plants were harvested at physiological maturity and grain yield was estimated on kg per ha basis. PROC GLM in SAS 9.3 (SAS Institute, 2012) was used to analyse the data collected. Blocks and rep were set as random effects in the analysis. The GCA and SCA effects of parents and crosses, respectively were estimated using the diallel SAS programme developed by Zhang et al. (2005) following Griffing's method 4 model 1 (fixed model), which involved F1s only (Griffing, 1956). The diallel model is presented in Equation 1 (Hallauer & Miranda, 1988) under the assumption that the combining ability effects: $\sum gi = 0$ and $\sum sij = 0$ for each j (Griffing, 1956):

$$Y\_ijk=\mu+ g\_i+ g\_j+ s\_ij+ \varepsilon\_ijk \text{ …….. [1]}$$

where,

Y_ijk=Observed value for the ijth cross in the kth replicate

μ=Grand mean

g_i and g_j=GCA effects of the *ith* and *jth* parent

s_{ij}SCA effects of the *ijth* cross

ε_{ijk} =Error term of the *ijth* cross in *kth* replication

The equation for the relative importance of GCA and SCA (Equation 2) was modified from Baker (1978) by Hung and Holland (2012).

$$\frac{2K^2\,GCA}{2K^2GCA+K^2SCA} \text{ …………………… [2]}$$

where, K^2GCA and K^2SCA are the variance effects of GCA and SCA, respectively. The closer this ratio is to 1, the better the predictability of hybrid performance using only GCA.

A base index selection (Equation 3) (Menkir & Kling, 2007; Badu-Apraku et al., 2011) was used to select lines from the two extremes of the distribution in order to identify productive single-cross hybrids under drought conditions.

$$I = [(2 \times YLI) + EPP - ASI - PASP - EASP - SG]$$
$$\text{……………………………………….. [3]}$$

where, YLI is the grain yield, EPP is the number of ears per plant, ASI is the anthesis silking interval, PASP is the plant aspect, EASP is the ear aspect and SG is the stay green characteristics.

RESULTS

Table 1 shows the GCA effect for grain yield and other agronomic traits. Two inbreds, TZdEEI 11 and TZdEEI 12, had significantly positive GCA effects for grain yield and in addition, TZdEEI 12 had a positive GCA for stay green characteristics and plant aspect. TZdEEI 4 and TZdEEI 5 had significant negative GCA effects for grain yield. TZdEEI 7 had a positive

GCA for yield, a negatively significant GCA for ASI and a negative GCA for ear aspect and a positive GCA for stay green characteristics. Also, TZEEI 79 had a negative and significant GCA for plant and ear aspect, negative GCA for ASI and stay green and a positive GCA for yield.

Table 1
GCA Effects of extra-early yellow inbred parents for grain yield and other agronomic traits evaluated under drought conditions

Parent	Days to Pollen	Days to Silking	Anthesis Silking Interval	Plant Height (cm)	Ear Height (cm)	Plant Aspect	Ear Aspect	Number of Ears per Plant	Stay Green	Grain Yield (kgha^{-1})
TZdEEI 1	0.15	-0.14	-0.29	10.25**	7.20**	-0.11	-0.08	0.01	0.08	-1.29716
TZdEEI 4	0.25	0.8*	0.55*	-4.67	-3.90	0.27	0.40*	-0.02	0.32	-689.72**
TZdEEI 5	-0.30	0.05	0.35	-11.42**	-7.20**	0.17	0.50**	-0.04	-0.03	-521.42**
TZdEEI 7	-1**	-1.55**	-0.55*	-4.12	-2.05	0.12	-0.05	0.03	0.07	270.8385
TZdEEI 9	1.4**	1.50**	0.10	-2.02	-0.95	-0.53**	0.15	0.01	-0.43*	-83.3947
TZdEEI 11	0.20	0.01	-0.19	5.50	6.05*	0.19	-0.38*	0.08**	-0.12	390.39**
TZdEEI 12	-0.30	-0.65	-0.35	-7.27	-3.65	0.37*	-0.30	0.00	0.58**	338.82*
TZdEEI 13	0.05	0.20	0.15	3.63	-0.25	-0.08	0.05	0.01	-0.38	-43.2878
TZEEI 58	0.8**	1.35**	0.55*	1.68	3.70	0.17	0.10	-0.04	0.07	-114.241
TZEEI 63	-0.20	-0.05	0.15	2.78	-2.55	-0.08	0.05	-0.01	0.07	133.9402
TZEEI 79	-0.05	-0.10	-0.05	11.53**	8.65**	-0.43*	-0.45**	-0.02	-0.08	82.03297
TZEEI 95	-1**	-1.40**	-0.40	-5.87	-5.05*	-0.08	0.05	-0.01	-0.18	237.3358
SE $\pm$	0.23	0.38	0.24	3.77	2.34	0.18	0.16	0.02	0.19	138.45
GCA	**	**	*	**	**	*	**	*	*	**

*=Significant at 5% level of probability, ** =significant at 1% level of probability, NS=not significant

The SCA effects for the 70 hybrids used in the study are presented in Table 2. TZdEEI 1 × TZEEI 58 and TZdEEI 5 × TZdEEI 11 had a significant positive SCA while TZdEEI 9 × TZdEEI 13, TZdEEI 1 × TZdEEI 12 and TZdEEI 5 × TZdEEI 12 had negative and significant SCA effects for grain yield.

Table 2
SCA effects of extra-early yellow single cross hybrids for grain yield and other agronomic traits evaluated under drought conditions

Hybrids	Days to Pollen	Days to Silking	Anthesis Silking Interval	Plant Height (cm)	Ear Height (cm)	Plant Aspect	Ear Aspect	Number of Ears per Plant	Stay Green	Grain Yield ($kgha^{-1}$)
TZdEEI 9 × TZdEEI 13	1.00	1.17	0.16	-21.17	-10.85	0.90	1.12*	-0.09	0.82	-989.01*
TZdEEI 1 × TZdEEI 12	1.10	2.66*	1.55*	-17.54	-9.09	0.03	0.70	-0.06	-1.13	-922.65*
TZdEEI 1 × TZEEI 58	-1.00	-1.84	-0.85	23.51*	8.06	-1.27*	-0.70	0.03	-0.63	881.93*
TZEEI 58 × TZEEI 63	1.86*	4.07**	2.21**	-22.02	-14.70	1.20*	1.67**	-0.43**	0.87	-2006.87**
TZdEEI 5 × TZdEEI 11	-1.45*	-2.69*	-1.25	13.36	4.11	-1.07	-0.80	0.07	-0.33	1262.57**
TZdEEI 5 × TZdEEI 12	0.05	0.47	0.41	-16.37	-3.70	1.25*	1.12*	-0.19**	1.47	-1020.45*
TZdEEI 7 × TZEEI 63	-0.85	-1.53	-0.69	0.28	4.05	-0.25	-0.68	0.05	-0.63	801.36
TZdEEI 12 × TZEEI 58	-0.55	-1.33	-0.79	3.53	3.40	0.25	-0.48	0.13*	0.87	744.93
TZdEEI 9 × TZdEEI 12	-0.65	-0.98	-0.34	10.23	-0.95	-0.55	-0.53	-0.01	-0.13	657.31
TZdEEI 4 × TZEEI 95	-0.80	-1.03	-0.24	16.48	6.40	-0.90	-0.63	-0.04	-0.13	580.28
TZdEEI 1 × TZdEEI 9	-0.10	-0.49	-0.40	20.21	19.21	-0.57	-0.25	0.05	-0.63	535.58
TZdEEI 13 × TZEEI 79	-0.55	-0.73	-0.19	19.78	9.55	0.30	-0.28	0.01	-0.03	525.51
TZdEEI 13 × TZEEI 63	0.10	-0.78	-0.89	6.53	-0.75	-0.05	-0.28	0.04	-0.18	460.85
TZdEEI 13 × TZEEI 95	0.40	0.57	0.16	4.18	3.25	-1.05	-0.78	0.02	-0.93	456.75
TZdEEI 11 × TZdEEI 12	-1.95**	-2.49*	-0.55	-2.79	-1.44	0.73	0.00	0.01	1.07	-382.78
TZdEEI 1 × TZdEEI 11	-0.40	0.09	0.49	-15.65	-13.33	-0.08	0.48	-0.09	0.09	-407.78
TZdEEI 5 × TZEEI 95	-0.25	0.72	0.96	-4.77	-4.80	-0.30	0.27	-0.02	-0.78	-444.09
TZdEEI 11 × TZdEEI 13	-0.30	1.16	1.45*	1.31	-0.34	-0.82	0.65	0.09	0.02	-513.86
TZdEEI 4 × TZEEI 79	0.75	0.67	-0.09	-0.92	-4.30	0.95	0.37	-0.08	0.77	-645.97
TZdEEI 7 × TZEEI 95	-0.05	-0.18	-0.14	-12.07	-2.45	-0.25	1.32**	-0.07	0.12	-707.74
SE $\pm$	0.7	1.13	0.71	11.26	7	0.55	0.49	0.06	0.57	413.62
SCA	*	NS	NS	NS	NS	NS	NS	**	*	NS

*=Significant at 5% level of probability, ** =significant at 1% level of probability, NS=not significant

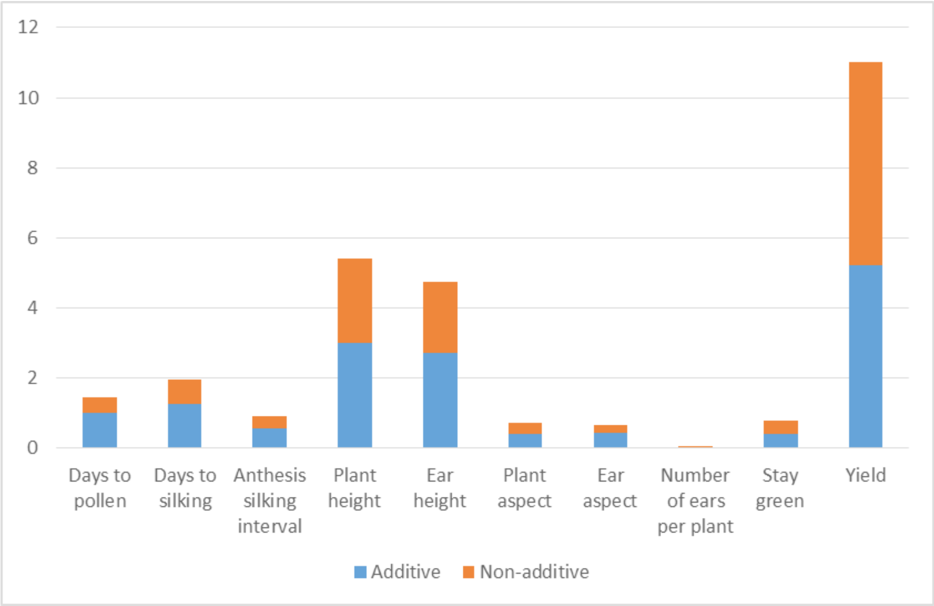

Figure 1. Gene action of some traits under drought conditions

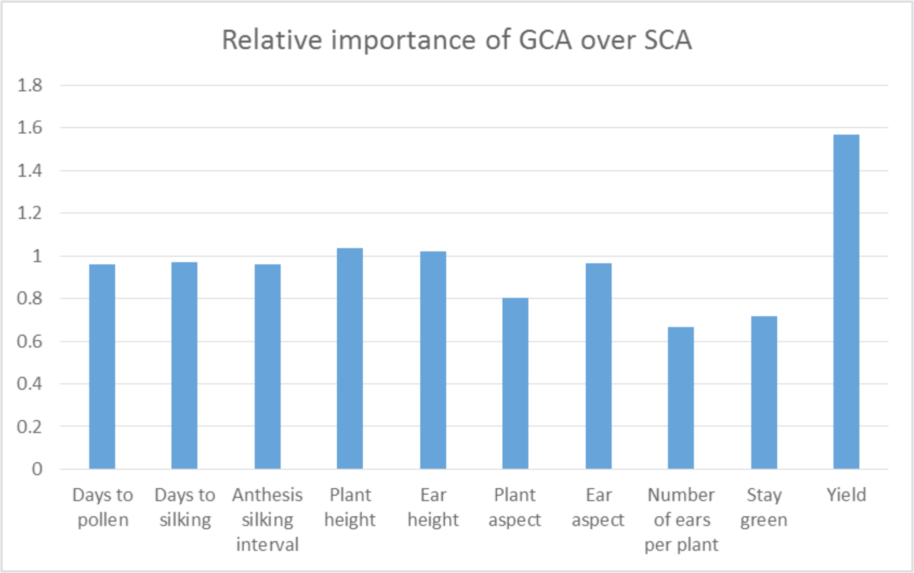

Figure 2. Relative importance of GCA over SCA

Figure 1 shows that the GCA mean squares were higher compared with those of the SCA for the measured traits excluding grain yield, with a higher SCA mean square than for GCA. The relative importance of the GCA over the SCA is presented in Figure 2. The values were closer to unity for all the traits except grain yield. From the correlation matrix (Table 3), negative correlations that were highly significant were observed between yield and ASI (-0.6), plant aspect (-0.33), ear aspect (-0.79) and stay green (-0.23). The positive correlation between plant aspect and ASI was not significant and the negative correlation between stay green and ASI was also not significant. However, a positive significant correlation was observed between ear aspect and ASI (0.52).

Table 3
Correlation between some traits of maize under drought conditions

	Days to Anthesis	Days to Silking	Anthesis Silking Interval (ASI)	Plant Height (cm)	Ear Height (cm)	Plant Aspect	Ear Aspect	Grain Yield (kgha^{-1})	Number of Ears per Plant (EPP)	Stay Green
Days to Anthesis	1									
Days to Silking	0.86**	1								
ASI	0.34**	0.77**	1							
Plant Height (cm)	-0.25**	-0.35**	-0.33**	1						
Ear Height (cm)	-0.12	-0.19*	-0.21*	0.77**	1					
Plant Aspect	0.09	0.08	0.04	-0.43**	-0.28**	1				
Ear Aspect	0.31**	0.50**	0.52**	-0.58**	-0.44**	0.29**	1			
Grain Yield (kgha^{-1})	-0.41**	-0.6**	-0.6**	0.52**	0.44**	-0.33**	-0.79**	1		
EPP	-0.2*	-0.3**	-0.31**	0.28**	0.27**	-0.23**	-0.38**	0.55**	1	
Stay Green	-0.04	-0.06	-0.06	-0.27**	-0.18*	0.66**	0.22**	-0.23**	-0.2*	1

*=Significant at 5% level of probability, ** =significant at 1% level of probability, NS=not significant

DISCUSSION

A higher ratio of GCA effects than that of the SCA effects were indications that potentially discriminating testers could be identified and the inheritance pattern was additive gene action. It can also be stated that the differences among the single-cross hybrids was the result of the GCA effects. This is similar to the report of Badu-Apraku et al. (2012) that GCA is dominant over SCA under stress conditions. For grain yield, the SCA was more important than GCA, indicating that the non-additive gene was more important than the additive gene in the inheritance pattern under drought stress. Badu-Apraku et al. (2013) also reported the preponderance of non-additive gene action than additive gene action for grain yield under drought stress. The SCA was more responsible for the differences among the diallel crosses for grain yield. This result also appears consistent with the findings of Guei and Wassom (1992), who reported that there was preponderance of non-additive over additive genetic effects for grain yield in maize under drought stress. With the exception of grain yield, the ratio of the relative importance of GCA over SCA was close to unity. Therefore, GCA can be used solely to predict the performance of specific hybrids in drought-prone areas or selection in drought environments.

From the correlation obtained in this study, ASI, plant aspect, ear aspect and stay green characteristics were negatively correlated with yield. Selection of hybrids with low ASI and low score for plant aspect, ear aspect and stay green characteristics will indirectly lead to selection of hybrids with higher yields. Also, a breeding objective can be directed towards improving these traits. From these correlations it can also be inferred that lines with negative GCA and SCA for ASI, plant aspect, ear aspect and stay green characteristics and positive GCA grain yield are mostly desirable and tolerant to drought. Such relationship has been previously reported by Bolanos and Edmeades (1996) and Badu-Apraku et al. (2011), who independently reported a strong negative correlation between these traits. The positive GCA recorded for TZdEEI 11 with respect to grain yield and a negative GCA for stay green characteristics indicated that this inbred line can combine with other inbred lines to produce high yielding hybrids under drought conditions and could also be used as testers. TZdEEI 12 had a positive GCA for yield and stay green characteristic, suggesting that this inbred line can also be used as a tester. The significant SCA values showed that hybrids can be selected as single cross testers with respect to a particular trait showing such significance. TZdEEI 1 × TZEEI 58 was found to be a tolerant single cross hybrid because it had a positive SCA for yield and negative SCA for ASI, plant aspect, ear aspect and stay green characteristics, while TZdEEI 9 × TZdEEI 13, TZdEEI 1 × TZdEEI 12, TZEEI 58 × TZEEI 63 and TZdEEI 5 × TZdEEI 12 were found to be susceptible single cross hybrids because they were the opposite of TZdEEI 1 × TZEEI 58.

CONCLUSION

In conclusion, additive gene action is more important in trait expression (with the exception of grain yield) than non-additive gene action in the set of hybrids used for this study. Also, performance of hybrids can be predicted using GCA solely. Anthesis silking interval, plant aspect, ear aspect and stay green characteristics were found to be traits that can be used for selection and improvement of grain yield of extra early maize in drought situations and could be used as indicators for drought tolerance. These traits were found to be significantly correlated to grain yield. The most promising genotypes identified in this study are TZdEEI 12 × TZEEI 63, TZdEEI 13 × TZEEI 95, TZdEEI 7 × TZEEI 79, TZdEEI 1 × TZEEI 58, and TZdEEI 1 × TZEEI 79, while the inbreds TZdEEI 11 and TZdEEI 12 were identified as good testers and TZdEEI 1 × TZEEI 58 was identified as a good single cross tester. The identified genotypes can be used to accelerate the breeding process for extra early maize varieties, commercialised as varieties after multi location trials and or shared with public breeding sectors.

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