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COMBINING ABILITY AND GENE ACTION FOR GRAIN YIELD AND RELATED TRAITS IN SOYBEAN (*Glycine max* (L.) Merrill) GENOTYPES

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ABSTRACT

The importance of soybean grain for human food, animal feed, protein, oil and industry is hindered in Nigeria by the absence of high-yielding improved varieties, emphasizing the need for enhanced variety to optimize yields. Ten hybrid soybean genotypes obtained from partial diallel crossing and their putative parents were evaluated on the field using randomized complete block design in three replications at the Research Farm of International Institute of Tropical Agriculture. High General Combining Ability was observed in TGx1987-62F for number of grains per pod, number of pods per plant and number of grains per plant. High GCA was also observed in TGx1989-19F for pod length, pod width, number of pods per plant and grain yield per plant. The most promising crosses that revealed high and positive Specific Combining Ability effect for grain yield were TGx1835-10E × TGx1987-62F, TGx1835-10E × TGx1988-5F and TGx1988-5F × TGx1989-19F. Narrow-sense heritability (HN) estimate was high for pod width, number of pods per plant and 100-grain weight. These traits could therefore, respond to selection. Genotypes such as TGx1989-19F and TGx1987-62F with high GCA and involved in crosses with high SCA for grain yield and yield-related characters could be considered for yield improvement in soybean.

Keywords: Diallel, Heritability, Mating, Combining Ability

INTRODUCTION

Soybean is one of the most important legume and oil-seed crops in Africa, particularly Nigeria. Its seed contains high quality protein (40%), oil (20%), and bioactive factors that can be used to substitute animal protein which is expensive for many households in Nigeria (Singh et al., 2008; Hartman et al., 2011).

Global and Africa average yields of soybean are generally higher than the average yield of 973.3kg/ha in Nigeria (FAOSTAT, 2017). This was attributed to the use of low yielding varieties, which is a problem that can only be resolved through concerted breeding effort. For soybean improvement, breeding methods like inter-varietal hybridization has helped to broaden the genetic base through

creation of variability (Bhatnagar and Karmakar, 1995).

Choice of parents is an important step towards hybridization program in soybean improvement. Some parental lines produce outstanding progenies from crossing with others; while others may not yield desirable progenies on crossing. Lines which perform well in several cross combinations are of great importance to plant breeders. It is therefore, necessary to use the knowledge of combining ability in selecting suitable parents for hybridization and identifying promising cross combinations. Combining ability analysis will also provide information on the nature and magnitude of various types of gene actions involved in the expression of quantitative characters (Machikowa et al., 2011). Such information is of potential use in formulating and executing an efficient breeding programme for achieving maximum genetic gain with minimum resources and time. This study was carried out to estimate combining ability and determine the nature of gene action for grain yield and yield related traits in soybean lines.

MATERIALS AND METHODS

Five soybean genotypes obtained from the Germplasm Unit of International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria on the basis of genetic variability for their grain yield (Table 1) were crossed in all possible combinations without reciprocals to obtain 10 F1 hybrids. A total of 10 F1 individuals and their five parents were evaluated using a randomized complete block design in three replications at IITA during the 2018 cropping season. IITA is located in the guinea savannah agro-ecology with latitude 7° 30'N, longitude 3° 54' E, altitude 227.2 m above sea level and an average rainfall of 1308 mm. Seeds were sown at the rate of one seed per hole with a spacing of 75 cm inter-row and 8 cm intra-row. Each entry was grown in a single row plot of 2 m length such that each plot contained 25 plants. Weeding was done as necessary but no insecticide and fertilizer was applied. Data were collected on ten selected plants per plot on number of pods per plant, number of grains per pod, number of grains per plant, pod length (cm), pod width (mm), 100-grain weight (g) and grain yield per plant (g).

Table 1: Soybean genotype, yield potential and year of release

Genotype	Average on-farm yield (Kg/ha)	Year of release
TGx 1989-19F	1.5-3.0	2014
TGx 1987-10F	1.5-2.5	2010
TGx 1988-5F	1.5-2.5	2014
TGx 1987-62F	1.5-2.5	2010
TGx 1835-10E	1.5-2.0	2008

Source: Soybean breeding unit, International Institute of Tropical Agriculture, Ibadan

Data Analysis

Plot means were analyzed for combining ability in the parents and F1s following

Griffings's method II (1956). Sum of squares and mean squares for GCA and SCA were calculated as follows:

$$SS_{GCA} = \frac{1}{n+2} \left[\sum (X_i + X_{ij})^2 + \frac{4}{n} Y^2 \dots \right]$$

$$SS_{SCA} = \frac{1}{2} \sum \sum X_{ij}^2 - \frac{1}{n+2} \sum (X_i + X_{ij})^2 \frac{2}{(n+1)(n+2)} Y^2 \dots$$

$$MS_{GCA} = SS_{GCA} / DF_{GCA}$$

$$MS_{SCA} = SS_{SCA} / DF_{SCA}$$

The general and specific combining ability effects were calculated as follows:

$$g_i = \frac{1}{n+2} \left[(X_i + X_{ij}) - \frac{2}{n} Y \dots \right]$$

$$s_{ij} = X_{ij} - \frac{1}{n+2} \left[(X_i + X_{ij}) + (Y_j + Y_{ij}) \right] + \frac{2}{(n+1)(n+2)} Y \dots$$

Where, n – number of parents, GCA – general combining ability, SCA – specific combining ability, SS_{GCA} – Sum of squares due to GCA, SS_{SCA} – Sum of squares due to SCA, X_{ij} – value of the cross between i^{th} and j^{th} parent, X_i – total of i^{th} (row) array in diallel table (summed over j), Y – grand total of parents and their crosses in diallel table, X_i – parental value of the i^{th} parent, MS – mean square, DF – degree of freedom.

Mean squares from the analysis of variance showing the effects of additive and dominance components were obtained according to Walter and Morton (1978). The dominance component b1 measuring directional dominance; b2 examining the difference between selfs and crosses among parents, and b3 measuring residual dominance variation, i.e. variation not yet accounted for by b1 and b2, were calculated. Genetic parameters for estimating the gene effects and parameter ratios in the parents and F1s of the diallel cross were obtained according to Hayman's method (1954). The genetic components include:

$$D = V_p - E$$

$$H_1 = V_p - 4\bar{W}r + 4\bar{V}r - (3n - 2) E/n$$

$$H_2 = 4\bar{V}r - 4V\bar{x} - 2E$$

$$F = 2V_p - 4Wr - 2(n - 2) E/n$$

$$h = 4(\bar{X}_p - \bar{X}_n) - 4(n-1) E/n^2$$

$$Fr = 2(V_p - \bar{W}r + \bar{V}r - Wr - Vr) - 2(n-2) E/n$$

$$\text{Mean degree of dominance} = \sqrt{\frac{H_1}{D}}$$

The proportion of genes with positive and

negative effects in parents = $\frac{H_2}{4H_1}$
 Number of group of genes controlling the characters and exhibiting dominance = $\frac{h}{H_2}$

Narrow and broad-sense heritability were calculated and expressed in percentage (Lush, 1940).

$$h^2_n = \left[\frac{\delta_A^2}{\delta_A^2 + \delta_D^2 + \delta_E^2} \right] \times 100$$

$$h^2_b = \frac{\delta_G^2}{\delta_P^2} \times 100$$

$$\delta_P^2 = \delta_A^2 + \delta_D^2 + \delta_E^2$$

$$\delta_G^2 = \delta_A^2 + \delta_D^2$$

Where, D = Component of genetic variance due to additive effects of the genes, H_1 = Component of genetic variance due to dominant effects of the genes, H_2 = Component of genetic variance due to dominant effects corrected for the genes distribution, F = The mean of Fr over the arrays, where Fr is the dominance effects in single array, h = Overall dominance effects of heterozygous loci. E

= Expected environmental components of non-heritable variation which is obtained from the analysis of variance for the design of experiment, i.e., $E = Me/b$, $h2n$ = narrow-sense heritability, $h2b$ = broad-sense heritability, $\delta2P$ = Phenotypic variance, $\delta2G$ = Genetic variance, $\delta2A$ = Additive variance, $\delta2D$ = Dominance variance, $\delta2E$ = Environmental variance.

RESULTS

Analysis of variance for combining ability revealed significant ($p < 0.01$) differences among the soybean genotypes for the characters evaluated except number of grains per pod (Table 2). The variability observed among the genotypes were further partitioned into General (GCA) and Specific (SCA) Combining Abilities. General combining ability (GCA) of the parents were significantly ($p < 0.01$) different for the characters evaluated. Significant ($p < 0.01$) difference was observed among the crosses with respect to number of pods per plant,

number of grains per plant, pod length, 100-grain weight and grain yield per plant. GCA to SCA ratio was greater than unity for pod width, 100-grain weight and number of pods per plant.

The estimates of GCA effects of parents used in this study revealed that TGx1989-19F had a desirable positive and significant GCA effect for pod length, pod width, number of pods per plant and grain yield per plant (Table 3). TGx1987-62F was, however, identified as the best general combiner for number of grains per pod, number of pods per plant and number of grains per plant. Genotypes TGx1987-10F and TGx1988-5F had negative and significant GCA effects for number of grains per pod, number of pods per plant and number of grains per plant. Cross TGx1987-62F \times TGx1989-19F had the highest SCA effect for number of pods per plant (Table 4). This was also evident in the two parents that make up this cross.

Table 2: Mean squares for general and specific combining ability of five soybean genotypes evaluated for grain yield and yield-related traits

Source of variation	Block (df = 2)	Genotype (df = 14)	GCA (df = 4)	SCA (df = 10)	Error (df = 28)	GCA/SCA
Pod length (cm)	0.10	0.12**	0.23**	0.09*	0.04	0.35
Pod width (mm)	0.90**	1.30**	3.92**	0.23*	0.08	2.63
Number of grains/pod	0.02	0.03	0.06**	0.03	0.01	0.28
Number of pods/plant	182.82	2720.48**	5062.82**	1191.29**	314.89	1.12
Number of grains/plant	1002.82	35201.09**	37398.56**	23930.16**	1704.01	0.16
100-grain weight (g)	8.26**	12.44**	32.61**	3.16*	1.20	1.60
Grain yield (g)	175.11*	283.60**	165.93*	257.65**	45.17	0.06

**,* Significant at 1% and 5% respectively

Table 3: General combining ability effects of five soybean genotypes evaluated for grain yield and yield related traits

Characters	P ₁	P ₂	P ₃	P ₄	P ₅
Pod length (cm)	-0.03	-0.12**	0.12**	-0.07	0.12**
Pod width (mm)	0.13*	-0.80**	0.36**	0.08	0.22**
Number of grains/pod	0.02	0.06*	-0.02	-0.09**	0.03
Number of pods/plant	-22.48**	32.19**	-18.25**	-8.75*	17.31**
Number of grains/plant	14.85	72.48**	-29.45**	-38.99**	10.81
100-grain weight (g)	0.10	-2.22**	1.26**	0.56*	0.30
Grain yield (g)	-3.30*	1.64	-2.79	0.78	3.67*

TGx1835-10E (P₁), TGx1987-62F (P₂), TGx1988-5F (P₃), TGx1987-10F (P₄), TGx1989-19F (P₅)

**,* Significant at 1% and 5% respectively

Table 4: Specific Combining Ability effects of soybean crosses evaluated for grain yield and yield related traits

Cross	Pod length (cm)	Pod width (mm)	Number of grains/pod	Number of pods/plant	Number of grains/plant	100-grain weight (g)	Grain yield/plant(g)
P ₁ × P ₂	-0.15	-0.08	-0.11*	11.14*	42.32*	0.11	12.45**
P ₁ × P ₃	0.04	0.10	0.01	25.83**	155.92**	-0.77	8.60**
P ₁ × P ₄	0.17	0.32*	0.04	-7.20	-41.88*	0.78	0.25
P ₁ × P ₅	0.03	0.09	0.04	3.98*	-29.01	0.89	-2.95
P ₂ × P ₃	0.22*	-0.13	-0.06	-15.46*	-129.41**	-0.43	-9.90**
P ₂ × P ₄	-0.05	-0.02	0.03	8.23*	-20.55	0.57	-1.25
P ₂ × P ₅	0.07	-0.06	0.11*	28.26**	-18.68	-0.01	2.99
P ₃ × P ₄	-0.10	0.04	-0.01	-15.59*	24.72	1.05*	4.55
P ₃ × P ₅	0.16	0.41**	0.09	-6.76	-0.75	1.30*	8.44*
P ₄ × P ₅	-0.02	0.09	-0.03	5.52	0.45	0.94	-2.29

P₁ - TGx1835-10E, P₂ - TGx1987-62F, P₃ - TGx1988-5F, P₄ - TGx1987-10F, P₅ - TGx1989-19F

Crosses TGx1835-10E × TGx1987-62F, TGx1835-10E × TGx1988-5F and TGx1835-10E × TGx1989-19F all had positive SCA effect for number of pods per plant. High and positive SCA effect for number of grains per plant were observed in crosses TGx1835-10E × TGx1987-62F and TGx1835-10E × TGx1988-5F. Crosses TGx1835-10E × TGx1987-62F, TGx1835-10E × TGx1988-5F and TGx1988-5F × TGx1989-19F were good specific combiner for grain yield per plant (Table 4).

Highly significant gene effects were observed for both additive (a) and dominance (b) for all traits except number of grains per pod (Table 5). However, (a) values were larger than (b) in all cases. Dominance component b₁ was significant with respect to pod length, pod width, number of pods per plant, 100-grain weight and grain yield per plant. Also, significant mean square values of b₂ component were observed for most of the traits except pod length and number of grains per pod. Dominance component b₃ was signifi-

cant with respect to all the traits observed except number of grains per pod.

Estimate of additive component (D) was larger than dominance components (H1 and H2) for pod width, number of pods per plant and 100-grain weight (Table 6). For all the traits evaluated, dominance component H1 was greater than H2. Average direction of dominance, represented by 'h' was positive for most of the traits evaluated except pod length and number of grains per pod.

Estimate of the frequency 'F' was negative for pod length, pod width and number of grains per pod. Dominance ratio $(H1/D)^{1/2}$ was less than unity for pod width, number of pods per plant and 100-grain weight. Broad-sense heritability (HB) estimates ranged from 0.71 for pod length to 0.95 for number of grains per plant. High narrow-sense heritability (HN) estimate was observed for pod width (68%), number of pods per plant (58%) and 100-grain weight (79%).

Table 5: Mean squares for additive, dominance effects and dominance components for seven traits following Walter and Morton (1978)

Source	Pod length (cm)	Pod width (cm)	Number of grains/pod	Number of pods/plant	Number of grains/plant	100-grain weight (g)	Grain yield/plant(g)
Rep	0.10	0.90**	0.02	182.82	1002.82	8.26**	175.11*
Additive (a)	0.37**	6.28**	0.11**	8096.37**	59837.69**	52.08**	265.48**
Domi-nance(b)	0.14**	0.35**	0.04	3760.07**	39620.90**	4.65**	405.97**
b1	0.42**	0.71**	0.05	2038.41*	853.45	15.14**	757.92**
b2	0.08	0.40**	0.04	7619.94**	47731.36**	3.74*	343.01**
b3	0.13*	0.24*	0.03	5216.51**	40886.02**	3.29*	385.95**
Error	0.04	0.08	0.02	308.19	1601.20	1.26	43.20

**,* Significant at 1% and 5% respectively

Table 6: Estimates of genetic parameters and ratios in the F₁ population of a half diallel cross observed for grain yield and yield related parameters (Hayman, 1954)

Parameters	Pod length (cm)	Pod width (cm)	Number of grains/pod	Number of pods/plant	Number of grains/plant	100-grain weight (g)	Grain yield/plant(g)
D	-0.31	0.54	-0.30	7038.99	41939.87	9.52	277.34
H ₁	-0.70	-0.42	-0.82	5971.34	51781.83	4.68	487.65
H ₂	-0.53	-0.33	-0.63	4489.00	38035.40	3.80	389.07
H	-0.08	0.01	-0.20	425.99	261.97	4.44	232.62
F	-0.42	-0.62	-0.38	4966.97	44197.60	0.53	325.09
E	0.01	0.05	0.01	102.03	552.42	0.56	17.94
$(H_1/D)^{1/2}$	1.50	0.88	1.65	0.92	1.11	0.70	1.33
h/H ₂	0.16	-0.02	0.31	0.10	0.01	1.17	0.60
H ₂ /4H ₁	0.19	0.20	0.19	0.18	0.18	0.20	0.20
H _N	0.18	0.68	0.27	0.58	0.38	0.79	0.21
H _B	0.71	0.92	0.75	0.94	0.95	0.87	0.84

D - additive variance, H1 and H2 - Dominance variances, h - Average direction of dominance, F - Frequency of dominance, E - Environmental variance, $(H1/D)^{1/2}$ - Average degree of dominance, $h2/H2$ - number of effective factors, $H2/4H1 (\pm UV)$ - Balance of positive and negative alleles.

DISCUSSION

Analysis of variance revealed significant differences among the 15 genotypes with respect to all of the characters evaluated, except number of grains per pod. This is an indication of inherent genetic variability among the genotypes used as parents. Presence of genetic variability among the genotypes necessitated further assessment through diallel analysis. Diallel analysis revealed that the genotypes used as parent in this study differed significantly with respect to grain yield and yield related characters. Significant SCA obtained for pod length, pod width, number of pods per plant, number of grains per plant, 100-grain weight and grain yield per plant is an indication that the five soybean genotypes behaved differently in cross combinations for these traits. Similar reports have been documented by Shankar et al. (2013). GCA: SCA ratio was greater for pod width, number of pods per plant and 100-grain weight. This suggests that additive component played greater role in the inheritance of these traits. The importance of additive gene action for the inheritance of number of pods per plant and 100-grain weight in soybean had been reported earlier by Otusanya et al. (2021), Umar et al. (2017) and Ghiday and Tizzazu (2017).

The general combining ability effects of five soybean genotypes were estimated to determine their genetic worth for use in production of superior progenies. It has been reported earlier by Ojo (2003) that entries with significant GCA effects (additive gene effects) could provide desirable genes for the improvement of characters under consideration. Thus, genotype TGx1989-19F

with high performance and high GCA effect for grain yield could be used as parent in hybridization programmes for improvement of the trait. TGx1987-62F was identified as the best general combiner for number of grains per pod, number of pods per plant and number of grains per plant and thus, can be used for improvement of these traits in soybean improvement program. Soybean genotypes with high GCA effect for yield and yield-related traits have been reported by Otusanya, et al. (2021) and Chiipanthenga et al. (2021). However, negative GCA effects associated with TGx1987-10F and TGx1988-5F for number of grains per pod, number of pods per plant and number of grains per plant make these two entries undesirable parents in the genetic improvement of the traits listed. Good general combining parents do not always show high SCA effects in their hybrid combinations. Thus, the information on GCA effects alone may not be sufficient to predict the extent of hybrid vigour by a particular cross combination. Therefore, information on GCA effects of parent needs to be supplemented with SCA effects of cross combinations.

Out of three high specific combiners identified for grain yield per plant, only one cross (TGx1988-5F \times TGx1989-19F) involved good \times poor general combiners as parents, while the remaining two crosses (TGx1835-10E \times TGx1987-62F and TGx1835-10E \times TGx1988-5F) involved poor \times average or poor \times poor general combiners as parents. According to Patil and Navale (2006), such result indicates the presence of allelic as well as non-allelic interaction in the expression of this character. High SCA effects observed in TGx1988-5F \times TGx1989-19F for pod

width, TGx1987-10F × TGx1989-19F for plant height, TGx1987-62F × TGx1989-19F for number of pods per plant and TGx1988-5F × TGx1989-19F for 100-grain weight involved good general combining parents. Hybridization between two good general combiners may be governed by additive × additive gene actions which might elicit transgressive segregants in the advanced generations for the traits, thus producing hybrids with good specific combining ability (Daniel et al. 2006). Conversely, cross TGx1835-10E × TGx1988-5F exhibited high SCA effects for number of grains per plant and number of pods per plant, though derived from parents that are poor general combiners. This suggests the presence of dominance or epistatic gene actions and an indication of genetic interaction between favorable alleles contributed by both parents (Adeniji and Kehinde, 2003). Otusanya et al. (2021) and Nassar (2013) have also reported crosses with good SCA effects for grain yield and yield-related traits.

Highly significant gene effects observed for additive and dominance for all traits analyzed except number of grains per pod confirmed the presence of both additive and dominance gene action in the expression of these traits. Among the dominance components, b1 was highly significant for most traits except number of branches per plant, plant height, number of grains per pod and number of grains per plant indicating that dominance was unidirectional, towards the better or higher parent in this study. The highly significant mean squares of the b2 component for plant height, pod width, number of pods per plant, number of grains per plant, 100-grain weight and grain yield per plant also suggest that the five soybean lines probably have unequal number of

genes (Ojo, 2003). The significant residual dominance effect of b3 component according to Ayo-Vaughan et al. (2013) is assumed to result from additive × dominance or dominance × dominance effects specific to each cross.

Among the dominance components (H1 and H2), a condition where H1 was greater than H2 ($H1 > H2$), as observed in this study, indicated that the positive and negative alleles at the loci for these traits were not equal in proportion (Adeniji and Kehinde, 2007). The positive estimates of average direction of dominance (h) for most of the analyzed traits except pod length and number of grains per pod confirmed that dominance was unidirectional and in the direction of the parent with higher expression of these traits (Ayo-Vaughan et al, 2013). The average degree of dominance $(H1/D)1/2$ was found in the range of over dominance for most of the characters except pod width, number of pods per plant and 100-grain weight which was found in the range of partial dominance. Knowledge of number of gene groups responsible for a particular trait is important for the genetic progress through selection. In the present study, the value of $h^2/H2$ was low for all the characters indicating that a few genes or group of genes generally controlled the inheritance of these traits. Chaudhari et al. (2013) and Patel et al. (2013) also reported similar results. The equal distribution of positive and negative genes in the parents helps breeder in selecting a particular desirable trait without losing other traits of interest. In the present study, asymmetrical distribution of positive and negative genes in the parental lines was observed from the estimate, $H2/4H1$ for all the characters. Asymmetrical distribution of alleles in the parents was also reported by Pandey and Singh (2010); Meena et al. (2010); Ushakumari et al.

(2010); Sharma et al. (2011); Ayo-Vaughan et al. (2013) and Kadam et al. (2013). Broad-sense heritability estimates were high for all the characters evaluated, indicating that there is less influence of environment on these traits. Also, narrow sense heritability (HN) estimates were high for number of pods per plant, pod width and 100-grain weight. Since HN shows the proportion of a trait that is transmitted from parents to their progenies, number of pods per plant, 100-grain weight and pod width with HN estimates of 58% or more were considered highly heritable according to this study because of their large GCA values (relative to SCA) and the prevalence of additive gene effects. It was observed that grain yield per plant and number of grains per plant that had low GCA value (relative to SCA) also had low estimates of HN. Thus, improvement of grain yield and yield related components in soybean will require a recurrent selection procedure to allow for favourable gene recombination in later generations before final selection is made (Ojo, 2003).

CONCLUSIONS

The seven soybean traits analyzed in this study were under additive and dominance gene effects. The preponderance of additive gene effects for pod width, number of pods per plant and 100-grain weight will enhance effective selection in early generations of segregating materials for these traits. Genotypes TGx1989-19F and TGx1987-62F with high GCA values and involved in crosses with high SCA for grain yield and yield related characters could be considered for yield improvement in soybean.

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