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Molecular Diversity and Identification of Heterotic Cross Combination for Seed Yield and its Related Characters in Soybean Genotypes, *Glycine max* (L.) Merrill

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Abstract

This study was carried out on the molecular diversity and identification of heterotic cross combination for seed yield and its related characters in soybean genotypes, *Glycine max* (L.) Merrill using SNP markers. The aim of the study was to assess the genetic diversity among the soybean genotypes based on SNP markers and to obtain information on the combining abilities of parents and the crosses and the gene actions involved in the expression in the various soybean yield contributing characters. The field experiment was laid out in a randomized complete block design (RCBD) with three replications. The result showed that mean square due to general combining ability (GCA) were highly significant for all the characters except Plant Height at Flowering and Number of Branches per Plant whereas in specific combining ability(SCA), the mean square was found significant in Days to Flowering, Plant Height at Flowering, Days to Maturity, Plant Height at maturity and Number of Seeds per Pod. Significant mean squares recorded in these characters indicated the importance of the additive and dominance gene effects in the expression and the inheritance of the characters. The GCA/ SCA ratio are more than unity for all the characters studied indicating that the additive genetic effect played an important role in the inheritance of the characters. Moreover, the promising general combiners were found in parents TGx 1990- 37F; TGx 1989-21F and TGx 1830 – 20E for Seed yield along with some other yield components. The promising hybrids were found in crosses TGx 1990 – 3F x TGx 1990 – 57F; TGx 1990- 37F x TGx 1830 – 20 E and TGx 1990- 37F x TGx 1990 – 57F for Seed Yield Plant along with some other yield components. At the molecular level, SNP markers were used to assess the extent of polymorphism among the F2 populations and the markers showed remarkable genetic diversity among the soybean genotypes.

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Keywords

Molecular diversity, heterotic cross combination, general combining ability, specific combining ability, soybean genotypes, SNP markers.

Introduction

Soybean, *Glycine max* (L.) Merrill belongs to the family Fabaceae. It is the most important leguminous seed crop among the oil crop plants, which accounted for 56% of global oil production in the international market in 2011. Presently, soybean is a world crop, cultivated widely in the United States of America, Brazil, Argentina, China and India. Soybean, grown primarily for the production of seed, has several uses in the food and industrial sectors, it represents one of the major sources of edible vegetable oil and proteins for livestock feed (Asafo-Adjei *et al.*, 2005). Among the grain legumes, soybean currently ranks third after groundnut and cowpea in terms of production and utilization (Asafo-Adjei *et al.*, 2005). Soybean seed contains about 38.50 - 45.80 %

protein, 15.84 – 30.00 % carbohydrate and 17.40 – 24.00 % oil (Asafo-Adjei, *et al.*, 2007). The use of soybean in rotation with cereals results in drastic reduction in striga seed bank in soils (Denwar and Ofori, 2003) thus, making it possible for such cereals to be grown with minimal or no striga attack.

Identification of superior genotypes is a goal of breeders. (Millioli *et al.,* 2018). Plant breeders often look for desirable genes and gene complexes (Glenn *et al.,* 2017); Identification of promising individuals is very important in any breeding program and great efforts have been directed to improve yield level and quality properties in crop plants (Kumar *et al.,* 2020).Understanding the genetic mechanism involved in the inheritance of a particular trait will help the plant breeder in effective selection and selecting for the best traits that would contribute to better yield (Lima *et al.,* 2019). Combining ability study provides information on the genetic mechanisms controlling quantitative traits and enables breeder to select suitable parents for further improvement (Kadam *et al.*, 2013). General combining ability is a good measure of additive gene action, whereas specific combining ability is a measure of non - additive gene action (Rojas and Sprague, (1952). Comprehensive analysis of the combining ability involved in the inheritance of quantitative characters and in the phenomenon of heterosis is necessary for the evaluation of various possible breeding procedure (Allard, 1960). Combining ability analysis also aids in the selection of desirable parents for heterotic crosses and also provides information about the effects of general combining ability (GCA) and specific combining ability (SCA) of parents, and is also helpful in estimating various types of gene actions (Griffing 1956; Falconer and Mackay, 1996). The choice of promising genotype from diverse genetic base and their subsequent utilization for hybridization is one of the strategies for improving the productivity of crops (Bohra *et al.*, 2020).

The selection of promising parents to obtain superior hybrids primarily depends on the predominance of the genes for the additive effect due to heterosis and heterobeltiosis (Beche *et al.,* 2013). Identifying parental combinations with strong heterosis for yield and genetic parameters are the most important steps in the development of new cultivars (Soughi *et al.*, 2019).

Genetic improvement of crop species is necessary to enhance their economic traits such as yield, resistance to abiotic and biotic stresses, etc. and thus forms the ultimate goal of plant breeding (Nair *et al.*, 2019). The conventional method used by plant breeders for selection is the phenotypic selection where morphological/phenotypic agronomic traits such as plant height; seed yields, etc are taken into account. However, most of them are controlled by many genes and follow quantitative inheritance and thus are highly influenced by environment (Wang *et al.,* 2018). They sometimes do not give correct picture of genetic make-up of the plants. In some cases, a trait may not express if suitable environment/condition is not available particularly in the case of stress related genes (Gupta *et al.*, 1999). Moreover, scoring of these markers is subjective, the results may differ when scored by different breeders. These constraints make the use of phenotypic markers limited (Sanghvi and Dave, 2017).

There are several different categories of markers that have been used to assist plant breeders in their crop genetic improvement programs. The markers are typically small regions of DNA, often showing sequence polymorphism in different individuals within a species and transmitted by the simple Mendelian laws of inheritance from one generation to the next. These include Restriction Fragment Length Polymorphism (RFLP) (Botstein *et al.*, 1980), DNA Amplification Fingerprinting (DAF) (Caetano *et al.*, 1991), Single Nucleotide Polymorphisms (SNP) (Jordan and Humphries, 1994), Microsatellite Simple Sequence Length Polymophism(SSLP), Amplified Fragment Length Polymorphism (AFLP) (Vos *et al.*, 1995), Amplicon Length Polymorphism (ALP) (Ghareyazie *et al.*, 1995). The efficiency of DNA based marker is so high to discriminate closely related varieties and even individuals of same species. They have proved their utility in various fields such as genetic diversity, genomic fingerprinting and mapping, population genetics, taxonomic studies and plant breeding programs (Adhikari *et al.*, 2017). In recent years, a novel class of markers named SNP has emerged as an important tool in genomics and are increasingly being used as molecular marker in various laboratory for different applications (Nadeem *et al.*, 2018). SNPs represent the most suitable because they occurred at high density within the genomes (Gaur *et al.*, 2012). Markers based on SNPs have rapidly gained the centre stage of molecular genetics during the recent years due to their abundance in the genomes and their amenability for high throughput detection formats and platforms (Mammadov *et al.*, 2012). SNPs possess unique merits that make them preferred over other classes of markers. Millions of SNPs have been generated in Soybean (Lam *et al.*, 2010), Arabidopsis (Zhang *et al.*, 2009), Rice (Subbaiyan *et al.*,

2012) and other crops (Delourme *et al.,* 2013) in order to enhance studies on marker assisted breeding or selection. The present study was carried out to assess the genetic diversity among the soybean genotypes based on SNP markers and to also obtain information on the combining abilities of parents and the crosses and the gene actions involved in the expression of the various soybean yield contributing characters.

Materials and Methods

The experimental materials for the present study consisted of seven genotypes collected from the soybean germplasm collection of the international institute of tropical agriculture, Ibadan, Oyo – State, Nigeria. The experiment was carried out in two phases. The first phase was the generation of the F_1s from the crossing of the parental lines following the half diallel mating technique. The F_1 seeds were later planted to generate the F_2 generations through self-pollination which were used for the molecular analysis. The second phase of the experiment was the molecular analysis using SNP markers. The field experiment was carried out on the Teaching and Research Farm of the Federal University of Technology, Akure, Ondo – State, Nigeria in year 2014 and 2015 respectively. The experiment was laid out in a randomized complete block design (RCBD) with three replications. A single row plot was adopted and each replication consisted of 28 plots (comprising the 7 parents and the 21 F_1 crosses). Fifteen plants were maintained per plot with an inter and intra row spacing of 60cm and 20cm respectively. Standard agronomic and plant protection treatment were carried out uniformly across the plots for the duration of the experiment. Data were collected on ten competitive mid – plants on the following agronomic characters: plant height at flowering (PHTF), days to flowering (DTF), number of branches per plant (NBP), plant height at maturity (PHTM), days to maturity (DTM), number of pods per plant (NPP), number of seeds per pod (NSP), total pod weight per plant (TPW) and seed yield per plant (SYP).

DNA Extraction

Total genomic DNA was extracted using the modified mini preparation protocol described by Dellaporta *et al.,* (1983) as follows: Approximately 200mg (0.2g) of lyophilized leaf sample was ground into fine powder. To each tube 700ul of hot (65^{o}C) plant extraction buffer (PEB) [containing 637.5ml of double distilled water (ddH_20), 100ml of 1M Tris-HCl (pH 8.0), 100ml of 0.5M ethylene diamine tetraacetic acid (EDTA) (pH 8.0), 100ml of 5M $NaCl_2$ and 62.5ml of 20% sodium dodecyl sulphate (SDS)] was added. One percent b-mercaptoethanol was added to the pre- warmed PEB just before use. The tubes were capped and inverted gently 6-7 times to mix the sample with buffer. The solution was incubated at 65°C in water bath for 20 mins with occasional mixing to homogenize the samples. After 20 mins, samples were removed from the water bath and uncapped. The tubes were allowed to cool at room temperature for 2 minutes after which 500ul of 5M of potassium acetate (CH_3COOK) was added to each tube and recapped. The tubes were then mixed by gently inverting 6-7 times and incubated on ice for 20 minutes. After 20 minutes of incubation on ice tubes were spun at 12,000 rpm for10 minutes at 4°C. The supernatant was transferred into new 1.5ml eppendorf tubes using wider bore pipette tips (1000 µl) and making sure debris were not taken along with the supernatant. 700µl chloroform isoamylalcohol was added to the supernatant and spun at 10,000 rpm for 10 minutes. The supernatant was transferred again into a new correspondingly labeled tubes and 700µl ice-cold isopropanol was added to each tube and mixed by gently inverting the tubes 6-10 times. The tubes were allowed to stand undisturbed in a rack and stored in a freezer (-20°C) for at least 1 hour or overnight to precipitate the DNA. After 1-hour precipitation in the freezer, the tubes were centrifuged at 12,000 rpm for 10 minutes at 4°C. The supernatant was carefully discarded with great care to disallow the pellet from dislodging from the bottom of the tube. The tubes were allowed to drain inverted on clean paper towels for 1 hour or more. The DNA pellets were washed twice in 100µl, cold 70% ethanol for 20 minutes and air dried completely. After drying, 60µl of 1×TE [10mM Tris-HCL (pH 8.0), 1mM EDTA (pH8.0)] was added to the pellets, followed by 2µl of 10ng/ml Rnase to remove the RNA. The solution was incubated for 40 minutes at 37°C with gentle mix at 10 minutes intervals.

SNP Analysis

SNP genotyping was done at Inqaba Biotechnical Industries (Pty) Ltd Pretoria, South Africa on the Mass ARRAY system from Agena Biosciences using the iPLEX reagents which included the iPLEX PCR, SAP, and iPLEX Extend following the iPLEX Gold Application Guide from Agena Biosciences (http://www.sequenom.com/Files/Genetic-Analysis-Graphics/iPLEXApplication/iPLEX-Gold-Application-Guide-v2r1) (Gabriel *et al.,* 2009; Masouleh *et al.,* 2009; Pattemore and Henry, 2008). The procedure of iPLEX PCR is the same as the normal PCR. Briefly, 10 ng genomic DNA was amplified in a 5µl reaction containing 1 x HotStarTaq PCR buffer (Qiagen), 1.625 mM $MgCl_2$, 0.5 mM each dNTP, 0.1µM each PCR primer, and 0.5 U Hot Star Taq DNA polymerase (Qiagen). The reaction was incubated at 94°C for 4 min followed by 45 cycles of 94°C for 20 s, 56°C for 30 s, 72°C for 1 min, and then followed by 3 min at 72°C. After iPLEX, excess dNTPs were removed from the reaction by adding 2 µl shrimp alkaline phosphatase (SAP) enzyme solution (1.53 µl water (HPLC grade), 0.17 µl SAP buffer (10x), 0.30 µl SAP enzyme (1.7 U/ µl)) into each sample well and mixed, and then incubated at 37°C for 20 minutes followed by 5 minutes at 85°C to deactivate the enzyme – called SAP procedure in iPLEX.

Extension Reaction

Extension Primers were synthesized at Inqaba Biotechnical Industries Pty Ltd. Pretoria South Africa. They were diluted to a stock concentration of 500 µM. This stock was split into a four-tier concentration grouping of 7µM, 9µM, 11µM and 14µM according to extension primer mass from smallest to largest. This four-tier system was used for Oligovalidation and peak optimisation on the Maldi-Tof Then, the iPLEX extend was carried out with a final concentration of between 0.625 and 1.5 l µM for each extension primer, depending on the mass of the probe, iPLEX termination mix (Agena Biosciences) and 1.35µM iPLEX enzyme (Agena Biosciences) and conducted a two-step cycles program; 94°C for 30 s followed by 40 cycles of 94°C for 5 s, then followed 5 cycles of 52°C for 5 s, and 80°C for 5 s within the 40 cycles, then 72°C for 3 min in the 40 cycles. The reaction was then desalted by addition of 6 mg resin to each well followed by mixing and centrifugation to settle the contents of the tube. The extension product was spotted onto a 96- well spectrochip before being flown in the MALDI-TOF (Matrix – Assisted Laser Desorption Ionisation Time of Flight) mass spectrometer (Agena Biosciences).

Bands were detected n UV-transilluminator and photographed by Gel documentation 2000, Bi o– Rad.

Results and Discussion

Analysis of variance for combining ability for all characters under study is presented in Table 2. The analysis of variance for combining abilities for various traits revealed that mean sum of squares due to general combining ability (gca) were highly significant ($P \leq 0.01$) for all the characters studied except plant height at flowering and number of branches per plant whereas the mean square for specific combining ability (sca) were highly significant ($P \leq 0.01$) for days to flowering, plant height at flowering, days to maturity, plant height at harvesting.

These indicated the importance of both additive and non-additive genes in expression of these characters. It was also evident that σ^2_{gca} was greater than σ^2_{sca} for all these characters indicating preponderance of additive gene action in expression of these characters.

Estimates of general combining ability (GCA) effects of the parents are presented in Table 3. For days to flowering, TGx 1990 – 57F followed by TGx 1990 – 37F exhibited highly significant negative GCA effects for this character (-1.61; -0.84). Highest positive GCA effects (1.33) was recorded in TGx 1990 – 55F. For plant height at flowering, the highest significant positive GCA effects was observed in TGx 1989 – 21F (3.91) followed by TGx 1990 – 55F (1.78). TGx 1990 – 57F had the highest negative GCA effects (-1.97) followed by TGx 1990 – 3F (-0.60).

For days to maturity, TGx 1990 – 57F exhibited highly significant negative GCA effect (-1.66) while the highest GCA effect (1.34) was recorded in TGx 1990 – 55F. For plant height at harvesting, the highest significant positive GCA effects was observed in TGx 1989 – 21F (7.20) followed by TGx 1835 – 40E (2.93) while TGx 1990 – 57F recorded the highest negative gca effect (-2.93).

As regards number of branches per plant, the highest gca effects was recorded in TGx 1835 – 40E (0.19) while the highest negative gca effects was recorded in TGx 1990 – 55F (-0.17).

As regards number of pods per plant, TGx 1830 – 20 E recorded the highest GCA effect (7.48) followed by TGx 1835 – 40E (3.98) and TGx 1990 – 37F (3.04) while the highest negative GCA effect was observed in TGx 1990 – 55F (-4.58).

As regards number of seeds per pod, the highest positive gca effect was recorded in TGx 1830 – 20 E (0.08) while the highest negative GCA effect was observed in TGx 1990 – 3F (-0.06).

For total pod weight, the highest positive gca effect was recorded in TGx 1830 – 20 E (4.66) followed by TGx 1990 – 37F (1.26) while the highest negative GCA effect was observed in TGx 1990 – 3F (-3.21)

In case of seed yield per plant, four of the parents exhibited GCA effects while three exhibited negative GCA effects. The highest positive GCA effect was recorded in TGx 1830 – 20 E (3.85) while the highest negative GCA effect was recorded in TGx 1990 – 3F (-2.52).

Estimates of specific combining ability (SCA) effects of the hybrids for the characters studied are presented in Table 4.

Eleven crosses displayed negative specific combining ability (sca) effects out of the twenty-one crosses for days to flowering. The highest negative SCA effects was observed in cross combination TGx 1835 – 40E x TGx 1990 – 57F (-1.91) followed by TGx 1990 – 3F x TGx 1830 – 20 E (-1.80) followed by TGx 1990 – 55F x TGx 1989 – 21F (-1.21).

As regards plant height at flowering, sixteen crosses displayed positive SCA effects being highest in TGx 1990 – 55F x TGx 1990 – 37F (5.52) and least in TGx 1835 – 40E x TGx 1989 – 21F (0.26). Highest negative SCA effect was observed in TGx 1990 – 3F x TGx 1990 – 57F (-3.00) followed by TGx 1835 – 40E x TGx 1990 – 55F (-2.44) while the least negative SCA effect was recorded in TGx 1990 – 55F x TGx 1990 – 3F (-0.29).

As regards number of branches per plant, thirteen crosses exhibited positive SCA effects. The highest positive SCA effect was recorded in TGx 1990 – 55F x TGx 1990 – 37F (P2 X P4) (0.55) while the highest negative SCA effect was recorded in TGx 1835 – 40E x TGx 1990 – 55F (P1 X P2) (-0.50).

Eleven crosses displayed negative SCA effects out of the twenty-one crosses for days to maturity. The highest negative SCA effects was observed in cross combination TGx 1835 – 40E x TGx 1990 – 57F (-1.94).

For plant height at harvesting, sixteen crosses displayed positive SCA effects. The highest positive SCA effects was observed in TGx 1990 – 55F x TGx 1990 – 37F (4.88) while it was least in TGx 1989 – 21F x TGx 1990 – 57F (0.05). Highest negative SCA effect was observed in TGx 1835 – 40E x TGx 1990 – 55F (-3.87) while it was least in TGx 1990 – 3F x TGx 1830 – 20 E (-0.28).

In case of number of pods per plant, the highest positive SCA effects was recorded in TGx 1990 – 37F x TGx 1830 – 20 E (14.00) followed by TGx 1990 – 3F x TGx 1990 – 57F (13.62) followed by TGx 1990 – 55F x TGx 1990 – 37F (10.71) whereas the highest negative SCA effects were observed in TGx 1990 – 55F x TGx 1990 – 3F and TGx 1990 – 55F x TGx 1990 – 57F (-4.18) followed by TGx 1835 – 40E x TGx 1990 – 3F (-2.39).

Concerning number of seeds per pod, nineteen crosses exhibited positive SCA effects being highest in TGx 1990 – 3F x TGx 1990 – 57F (0.16).

As regards total pod weight, sixteen crosses exhibited positive SCA effects, the highest positive SCA effect was recorded in TGx 1990 – 3F x TGx 1990 – 57F (9.44).

As regards seed yield per plant, sixteen of the crosses displayed positive SCA effects being highest in cross TGx 1990 – 3F x TGx 1990 – 57F (7.44) whereas the highest negative SCA effect was observed in TGx 1990 – 55F x TGx 1830 – 20 E (-3.57).

The levels of polymorphism for the F2 population of Soybean by SNP markers are presented in Table 5. 32 SNP primers were used to differentiate among the F_2 population.

A total of 322 bands were recorded. 214 of them were polymorphic (66.45%) and 108 were monomorphic (33.55%). the number of amplified band per primer ranged from 3 to 15 bands a maximum number 15 bands were amplified by BARC – 030337- 06857, BARC – 040459 – 07745 and BARC –041267- 07957 while a minimum number of 3 bands was amplified by the primer BARC –018933 – 03040.

The highest polymorphism % (100%) was recorded by primer BARC – 014847 – 01910 and BARC –030337 – 06857 and lowest (0%) was recorded in BARC –018933 – 03040 and BARC –041819 – 08107.

In the present study, GCA variances were significant for all the characters with the exception of plant height at flowering and number of branches per plant.

The significant GCA mean square among the characters indicated variability of GCA among the parents. Significant mean square for GCA in number of pods per plant, number of seeds per pod and pod length per plant has been reported by Nassimi *et al.*, (2006); Akbar *et al.*, (2008) and Liang *et al.*, (2019). Significant mean square for GCA in days to flowering has also been reported by Arunga, (2010) and Golkar, (2017).

Table.1 The Names and Source of Soybeans, Glycine max Genotypes

Parental No	Genotype Name	Source
1	TGx1835 – 40E	International Institute
2	TGx1990 – 55F	of Tropical Agriculture
3	TGx1990 – 3F	(IITA) Ibadan, Oyo, State, Nigeria
4	TGx1990 – 37F	
5	TGx1989 – 21F	
6	TGx1830 – 20 E	
7	TGx1990 – 57F	

Table.2 Analysis of Variance for general combining ability (GCA) and specific combining ability (SCA) for various characters in Soybean, Glycine max across two cropping years

SOV	Df	DTF (days)	PHTF (cm)	NBP	DTM (days)	PHTH (cm)	NPP	NSP	TPW (g)	SYP (g)
Year	1	12630.90**	6093.09**	160.74*	124579.40**	108102.30**	200137.40**	5.12**	42194.04**	24544.38**
Rep (Year)	4	4.72	281.52**	35.10**	4.61	171.10**	6826.95**	0.65**	2735.13**	697.70**
GCA	6	96.36**	374.93	1.43	98.80**	1083.49**	1671.26**	0.17**	516.51**	377.75*
SCA	21	20.36**	42.68**	1.33	20.46**	60.57**	655.05	0.10*	274.30	167.17
Error	108	5.48	14.42	1.63	5.44	19.49	279.55	0.05	90.95	62.00
GCA/SCA		4.73	8.78	1.08	4.83	17.89	2.55	1.70	1.88	2.26

*, ** significance at 5% and 1% level of probability respectively

SOV= Source of Variation; GCA= general combining ability; SCA= specific combining ability DTF=Days to flowering (days); PHTF= Plant Height at Flowering (cm);NBP= Number of Branches per Plant; DTM = Days to Maturity(days); PHTH = Plant Height at Harvesting (cm);NPP = Number of Pods per Plant; NSP = Number of Seeds per Pod; PL = Pod Length per Plant (cm); TPW = Total Pod Weight (g); SYP = Seed Yield per Plant (g)

Table.3 Estimates of General Combining Ability (GCA) Effects of Parents in Soybean, *Glycine max*

PARENTS	DTF (days)	PHTF (cm)	NBP	DTM (days)	PHTH (cm)	NPP	NSP	TPW (g)	SYP (g)
P1	0.17	1.63**	0.19	0.15	2.93**	3.98	0.03	0.75	0.01
P2	1.33**	1.78**	-0.17	1.34**	2.10**	-4.58*	-0.04	-1.62	-1.94
P3	0.86*	-0.60	-0.04	0.88*	-0.90	-3.70	-0.06*	-3.21*	-2.52*
P4	-0.84*	-0.36	0.01	-0.82*	-1.19*	3.04	0.03	1.26	1.29
P5	0.77*	3.91**	0.18	0.76*	7.20**	1.91	0.01	0.04	0.58
P6	-0.67*	1.13**	0.08	-0.65*	1.34*	7.48**	0.08**	4.66**	3.85**
P7	-1.61**	-1.97**	0.03	-1.66**	-2.93**	0.17	0.01	-0.37	-0.12
SE (gi)	0.24	0.38	0.13	0.24	0.45	1.69	0.02	0.96	0.80
SE (gi-gj)	0.36	0.59	0.20	0.36	0.68	2.58	0.03	1.47	1.22

*, ** significance at 5% and 1% level of probability respectively

DTF= Days to flowering (days); PHTF= Plant Height at Flowering (cm); NBP= Number of Branches per Plant; DTM = Days to Maturity (days); PHTH == Plant Height at Harvesting (cm);NPP = Number of Pods per Plant; NSP = Number of Seeds per Pod; TPW = Total Pod Weight (g); SYP = Seed Yield per Plant (g);

P1= TGx 1835 – 40E; P2= TGx 1990 – 55F; P3 = TGx 1990 – 3F; P4 = TGx 1990 – 37F; P5 = TGx 1989 – 21F; P6 = TGx 1830 – 20 E;P7 = TGx 1990 – 57F.

Table.4 Estimates of Specific Combining Ability (SCA) Effects Hybrids of Soybean, Glycine max

Hybrids	DTF (days)	PHTF (cm)	NBP	DTM (days)	PHTH (cm)	NPP	NSP	TPW (g)	SYP (g)
P1x P2	-0.79	-2.44*	-0.50	-0.76	-3.87**	3.47	0.07	0.96	0.86
P1x P3	-0.18	1.86	0.19	-0.16	2.65*	-2.39	-0.06	-0.91	0.19
P1x P4	1.13	1.01	-0.17	1.21	1.72	0.83	0.02	0.39	0.34
P1x P5	0.40	0.26	-0.05	0.19	0.15	3.82	0.05	1.40	1.24
P1x P6	1.51*	0.90	0.03	1.52*	1.19	1.65	0.01	1.19	1.32
P1x P7	-0.91	2.32*	0.47	-0.91	2.51*	3.02	0.00	2.33	1.94
P2x P3	-1.91*	-0.29	-0.01	-1.94*	-3.00**	-4.18	-0.03	-0.14	-0.06
P2x P4	0.57	5.52**	0.55	0.53	4.88**	10.71*	0.08	3.97	2.45
P2x P5	-1.21	-0.76	0.33	-1.19	-0.63	3.33	0.05	3.15	3.35
P2x P6	-0.67	1.10	0.35	-0.68	0.31	-2.64	0.00	-3.82	-3.57
P2x P7	0.40	0.64	0.30	0.45	0.70	-4.18	0.00	0.15	-1.39
P3x P4	-0.28	1.34	-0.33	-0.29	0.41	-1.90	0.00	-1.44	-1.32
P3x P5	2.64**	0.78	-0.45	2.66**	0.31	3.13	0.08	3.21	2.57
P3x P6	-1.80*	-0.37	-0.17	-1.82*	-0.28	-1.12	0.01	-0.58	-0.89
P3x P7	-0.64	-3.00**	0.36	-0.59	-2.41*	13.62**	0.16*	9.44**	7.44**
P4x P5	0.03	0.85	0.34	0.05	0.46	0.60	0.01	0.43	0.60
P4x P6	0.23	1.04	0.04	0.22	2.01	14.00**	0.15*	8.57**	6.37**
P4x P7	-0.53	1.70	-0.09	-0.56	0.78	7.35	0.08	5.24**	4.45*
P5x P6	-0.88	0.84	0.02	-0.87	0.68	2.93	0.05	2.71	1.92
P5x P7	0.17	0.55	0.03	0.26	0.05	5.95	0.09	3.74	4.29*
P6 x P7	1.27*	1.34	0.42	1.33*	2.36*	3.59	0.04	2.57	0.10
SE (Sij)	0.59	0.95	0.32	0.59	1.11	4.19	0.06	2.39	1.98
SE (Sij – Skl)	0.81	1.31	0.44	0.80	1.52	5.77	0.08	3.30	2.72

*, ** significance at 5% and 1% level of probability respectively

DTF= Days to flowering (days); PHTF= Plant Height at Flowering (cm); NBP= Number of Branches per Plant; DTM = Days to Maturity (days); PHTH == Plant Height at Harvesting (cm);NPP = Number of Pods per Plant; NSP = Number of Seeds per Plant; TPW = Total Pod Weight (g); SYP = Seed Yield per Plant (g);

P1= TGx 1835 – 40E; P2= TGx 1990 – 55F; P3 = TGx 1990 – 3F; P4 = TGx 1990 – 37F; P5 = TGx 1989 – 21F; P6 = TGx 1830 – 20 E; P7 = TGx 1990 – 57F.

Table.5 Levels of polymorphism for F_2 populations of Soybean, *Glycine max* by SNP- PCR analysis

PRIMER NAME	NUMBER OF BANDS	POLYMORPHIC BAND	MONOMORPHIC BAND	POLYMORPHIC %	MONOMORPHIC %
BARC-013065-00437	9.00	6.00	3.00	66.67	33.33
BARC-014847-01910	10.00	10.00	0.00	100.00	0.00
BARC-015973-02029	9.00	6.00	3.00	66.67	33.33
BARC-016485-02069	10.00	7.00	3.00	70.00	30.00
BARC-016861-02355	9.00	6.00	3.00	66.67	33.33
BARC-018933-03040	3.00	0.00	3.00	0.00	100.00
BARC-019085-03298	10.00	7.00	3.00	70.00	30.00
BARC-021329-04038	10.00	7.00	3.00	70.00	30.00
BARC-021827-04218	10.00	7.00	3.00	70.00	30.00
BARC-021831-04219	12.00	9.00	3.00	75.00	25.00
BARC-021937-04237	9.00	6.00	3.00	66.67	33.33
BARC-024043-04709	10.00	7.00	3.00	70.00	30.00
BARC-024333-04850	12.00	9.00	3.00	75.00	25.00
BARC-025961-05189	8.00	5.00	3.00	62.50	37.50
BARC-028309-05824	9.00	6.00	3.00	66.67	33.33
BARC-028793-06015	13.00	7.00	6.00	53.85	46.15
BARC-029343-06156	9.00	6.00	3.00	66.67	33.33
BARC-029859-06448	10.00	7.00	3.00	70.00	30.00
BARC-030337-06857	15.00	15.00	0.00	100.00	0.00
BARC-030735-06928	9.00	6.00	3.00	66.67	33.33
BARC-030807-06945	12.00	6.00	6.00	50.00	50.00
BARC-031701-07215	9.00	6.00	3.00	66.67	33.33
BARC-039561-07508	9.00	6.00	3.00	66.67	33.33
BARC-039593-07509	12.00	6.00	6.00	50.00	50.00
BARC-040033-07641	9.00	6.00	3.00	66.67	33.33
BARC-040075-07652	12.00	9.00	3.00	75.00	25.00
BARC-040339-07714	12.00	6.00	6.00	50.00	50.00
BARC-040459-07745	15.00	9.00	6.00	60.00	40.00
BARC-041267-07957	15.00	9.00	6.00	60.00	40.00
BARC-041819-08107	3.00	0.00	3.00	0.00	100.00
BARC-042201-08212	9.00	6.00	3.00	66.67	33.33
BARC-044047-08593	9.00	6.00	3.00	66.67	33.33
	322.00	214.00	108.00		

The GCA variance were higher than the SCA variance which suggested the predominance of the additive and additive x additive gene actions in the inheritance and expression of the characters considered in the present material (Hange and Pawar, 2020). However, the effects of the non-additive gene action (dominance) revealed by significant SCA mean squares cannot be underemphasized. The significant GCA and SCA mean square for some of the studied characters showed the importance of both additive and dominance gene effects. The results of this finding are in agreement with the findings of Akrami and Arzani (2019). They observed that mean squares due to GCA and SCA were highly significant for days to flowering, plant height and days to maturity. The ratio of gca/sca variance was greater than unity for all the characters in the present study. This indicates the preponderance of additive genetic variance (Amiri-oghan *et al.,* 2009). This suggested greater importance of additive gene action in their expression and indicated very good prospect for the exploitation of additive genetic variation for the characters in soybean yield through hybrid breeding (Su *et al.,* 2017). Suggesting that the major portion of genetic variability in the base population was additive in nature (Joshi *et al.,* 2018). It also suggests greater importance of additive gene action in the expression and indicates very good prospect for the exploitation of additive genetic variation for yield and its component characters in soybean through hybrid breeding (Manjeet *et al.,* 2020). Although there was a preponderance of additive gene action for all characters, the presence of a considerable amount of non-additive gene action could not be totally neglected (Noubissie *et al.,* 2019). Evidence that both additive and non-additive gene effects are involved in the genetic control of the characters investigated implies that both gene effects should be considered when developing breeding schemes for the selection of superior lines (Aladji *et al.,* 2018). The significant mean squares for GCA and SCA obtained for these characters suggest that the parents and their hybrids in the diallel crosses were highly variable for these characters (Kaushik *et al.,* 2018). In addition, a large proportion of total variability among the hybrids in the current study resulted from gene actions with predominantly additive effects. This is a desirable phenomenon necessary for greater crop improvement, especially when quantitative traits are concerned. Though the results from this study revealed that majority of characters are governed by additive genes and partially by non- additive gene action, selection in such promising population could be effective in early generations (Makhdoom *et al.,* 2019).Soybean breeders are very much interested in determining the genetic potential of their inbred parents in hybrid combination for two major reasons. Firstly, by identifying the parents which produce good progenies in specific combinations and secondly, by identifying the parents which form good combinations with series of other parents (Li *et al.,* 2019). Parents presenting higher gca must be preferred to be part of crossing programmes for the selection of promising homozygous lines (Ahmad *et al.,* 2013). The gca effects are attributable to additive and additive x additive gene effects. The predominance of the additive gene effect suggests that the best progeny might be derived from crosses with genotypes having the greatest positive gca (Teodoro *et al.,* 2019). Therefore, crosses involving genotypes with greater estimates of gca should be potentially superior for the selection of lines in advanced generations (Kulkarni *et al.,* 2020). The hybrid combinations exhibiting high specific combining ability effects for yield and yield related traits were also involved with parents having high x high, high x low and low x low gca effects (Latha *et al.,* 2018). The involvement of at least one parent with high gca effects and other parents with high or average or low gca effects was also reported by Tripathi *et al.,* (2012). These results indicated the involvement of both additive and non – additive genetic effects for the expression of these characters. The crosses having high sca for seed yield with other agronomic characters need to be selected and evaluated to serve as basis for isolating desirable hybrids for soybean breeding programmes.(Nirala *et al.,* 2018). It is noteworthy to know that sca effect alone has limited value in the choice of parent in breeding programmes for self-pollinated crops like soybean (Cruz and Regazzi, 1994). The sca effect would be used in combination with other parameters, such as the hybrid mean value of a trait and the gca of the respective parents. Thus, hybrid combinations with high means, favourable sca estimates and involving at least one of the parents with high gca would tend to increase the concentration of favourable alleles (Golkar *et al.,* 2017). Hybridization between two good general combiners may be governed by additive x additive gene actions which might be utilized in the advanced generations for the traits thus producing hybrids with good specific combining ability (Daniel *et al.,* 2006). On the other hand, the crosses exhibiting good sca effect though derived from parents that are poor general combiners suggest the presence of dominance or epistatic gene actions and an indication of genetic interaction between favourable alleles contributed by both parents (Adeniji and Kehinde, 2003; Torche *et al.,* 2018). The negative estimates of sca values recorded in this study is indicative of a partial dominance situation across loci (Adeniji and Kehinde, 2007). However, highly significant sca effects do suggest that non - additive gene action (dominance and additive x dominance gene effects) could play a vital role in the improvement of soybean for the traits of concern (Susanto, 2018). The breeder is therefore interested in combinations with the most favourable estimates of sca which involve at least one parent that presented the most favourable effect of gca (Mwale *et al.*, 2017). SNP markers have proven to be a powerful tool for molecular genetic analysis and plant breeding programs to assess genetic diversity for the development of improved varieties (Su *et al.*, 2018). This gives an insight into the genetic diversity and polymorphism among the F_2 population and the possibility of their further use in soybean breeding programs.

There was a wide genetic variability among the F_2 populations from the result of the SNP markers analysis. This will provide a good opportunity for selection among the F_2 populations to serve as a possibility for their utilization in further soybean breeding program. The significant GCA and SCA observed in some of the characters studied indicates that the expression of the characters was under the influence of both additive and dominance gene action. The GCA variances were comparatively higher than SCA emphasizing the importance of additive gene effects in controlling these characters in the present material. GCA effects of the parents indicated that genotypes TGx 1830 – 20 E, TGx 1990 – 37F and TGx 1989 – 21F were promising general combiners for seed yield along with some other yield components in soybean due to their high and positive GCA effects. It also suggests greater concentration of positive genes with additive or additive x additive gene effects in these parents. For these characters therefore, for the improvement of yield and its components, these parents could be exploited in cross combination in soybean improvement programmes. From the SCA effects of the studied characters; cross combinations TGx 1990 – 3F x TGx 1990 – 57F; TGx 1990 – 37F x TGx 1830 – 20 E and TGx 1990 – 37F x TGx 1990 – 57F were seen as promising hybrids for seed yield along with some other yield components. Hence, these parents along with the cross combinations may be considered as potential materials to be utilized for hybridization and selection in soybean breeding programmes.

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