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Gene Action for Yield and Yield Attributes by Generation Mean Analysis in Groundnut (*Arachis Hypogaea* L.)

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Abstract

Genetic studies assist the breeder in understanding the inheritance mechanism and enhance the efficiency of a breeding programme. Knowledge of the way genes act and interact will determine the breeding system that optimizes gene action more efficiently and will elucidate the role of breeding systems in the evolution of crop plants. The generation mean analysis was employed in four crosses viz., CO 7 × GPBD 4, ICGV 03128 × GPBD 4, ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6 of groundnut to partition the genetic variance into additive, dominance and epistasis. Hence F1, F2 and F3 generations of each cross were evaluated along with their parents to assess the nature of gene action involved for various characters which in turn helps in formulating an effective and sound breeding programme in groundnut. In all the vegetative and reproductive characters, additivity, dominance and one or more of the epistatic effects determined the expression. Pedigree method of breeding followed by simple selection in later generation would be a meaningful breeding strategy to be followed in such crosses for the improvement of the characters under evaluation. Considering the kernel yield per plant, pod yield per plant and foliar disease incidence, the cross ICGV 03128 × GPBD 4 was adjudged as the best cross for further selection programme.

Highlights

- Groundnut is an important oilseed crop and a principle source of human nutrition in arid and semi-arid regions of the world.
- Choice of appropriate breeding procedure depends on the type of gene action involved in the expression of the characters in a genetic population.
- Generation mean analysis was employed to study the genetics of yield and its components in each of the four cross combinations in groundnut.
- In all the vegetative and reproductive characters, additivity, dominance and one or more of the epistatic effects determined the expression.
- Pedigree method of breeding followed by simple selection in later segregating generations will be a meaningful breeding strategy to be followed.
- Based on the yield and foliar disease incidence, the cross ICGV 03128 × GPBD 4 was adjudged as best for further selection programme.

Keywords: Groundnut, gene action, generation mean analysis, five parameters, yield, yield attributes

Groundnut (*Arachis hypogaea* L.) is a vital food and cash crop for resource-poor farmers in Asia and Africa. It can be consumed and utilized in diverse ways due to its nutritional, medicinal and fodder values. Though the groundnut crop has morphological, biochemical, physiological variability, it has narrow genetic base because of its monophyletic origin, lack of gene flow due to ploidy barrier and self-pollination (Mondal *et al.*, 2007). Genes are the functional units that govern the development of various characters of an individual. Gene action refers to the behavior or mode of expression of genes in a genetic population and the understanding of gene action is of paramount importance to plant breeders. Knowledge of gene action in plant breeding helps in selection of parents for use in the hybridization programmes, in choice of appropriate breeding procedure for the genetic improvement of various quantitative characters and also in estimation of some other genetic parameters. Gene action is measured in terms of components of genetic variance and is of three types, *viz*., additive, dominance and epistatic gene action. Additive genetic variance is a pre-requisite for genetic gain under selection, because this is the only genetic variance which responds to selection. In addition to additive variation, it has been suggested that non-additive variance (dominance and epistasis) may also be involved in the inheritance of many quantitative characters in groundnut (Wynne, 1976). In spite of the limited scope of exploitation of non-allelic interactions in groundnut, the information on non-allelic interactions would be of value to groundnut breeders to formulate appropriate breeding procedures. The variation due to dominance effects and their interactions cannot be exploited effectively in crops like groundnut while the additive type of epistasis is potentially useful, as it can be fixed in homozygous cultivars. Hence insight into the nature of gene action involved in the expression of various characters is essential to a plant breeder for starting a judicious breeding programme.

Materials and methods

Study area

The experiment was conducted at Oilseeds Farm, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore, during *Rabi* 2013-14.

Experimental material

The material for this study comprised of four crosses *viz*., CO 7 × GPBD 4, ICGV 03128 × GPBD 4, ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6. Crosses were made between six released/ advanced breeding lines *viz.*, CO 7, ICGV 00350, ICGV 03128, TMV 2, TMV Gn 13, VRI 2 and three testers *viz.*, COG 0437, GPBD 4, VRI Gn 6 in order to develop foliar disease resistant genotypes with high yield. The parents were crossed in line × tester mating fashion to synthesize 18 F_1 hybrids. Based on combining ability and heterosis studies for kernel yield per plant, pod yield per plant and foliar disease resistance, four crosses *viz*., CO 7 × GPBD 4, ICGV 03128 × GPBD 4, ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6 were selected and further advanced to assess the nature of gene action by generation mean analysis. Generations *viz*., P_1, P_2, F_1, F_2 and F_3 populations in each cross were developed to study the genetic interactions. The spacing adopted was 30 × 10 cm and the recommended cultural practices were followed throughout the crop growing period.

Observations recorded

Observations were recorded on 12 characters *viz*., plant height (cm), number of primary branches, number of pods per plant, 100-pod weight (g), 100-kernel weight (g), shell weight (g), shelling percentage, sound mature kernel (SMK) (%), pod yield per plant (g), kernel yield per plant (g), late leaf spot (LLS) and rust score. In order to screen the lines for sources of resistance to late leaf spot and rust, nine point disease scale suggested by Subrahmanyam *et al.* (1995) were utilized.

Statistical analysis

Action of the genes controlling quantitative characters can be described by the use of gene models. Mean of five generations *viz*., P_1, P_2, F_1, F_2 and F_3 were used to estimate genetic parameters following a perfect fit solution given by Cavalli (1952). The mid-parental effect (m) and the types of gene action *viz*., additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) were determined using five parameter model of generation mean analysis. The adequacy of simple additive-dominance model was detected by employing C and D scaling test suggested by Mather and Jinks (1971). The additive-dominance model was considered inadequate when any one of the two scales was found to deviate significantly from zero.

Results and discussion

A good knowledge on the genetic systems controlling expression of the characters facilitates the choice of the most efficient breeding and selection procedure (Gopikannan and Ganesh, 2013; Mangaldeep *et al.*, 2015). The generation mean analysis with first degree statistics were adopted to detect non-allelic interaction component of the mean of the phenotypic distribution. Mean of five generations *viz.*, P_1, P_2, F_1, F_2 and F_3 of each cross are presented in Table 1 and the results of scaling test and genetic parameters in each cross (Table 2) are discussed character wise, hereunder.

Table 1: Mean and standard error of various generations involved in generation mean analysis

Cross	P_1	P_2	F_1	F_2	F_3
Plant height (cm)					
CO 7 × GPBD 4	12.13±0.40	10.38±0.63	11.34±0.96	15.32±0.44	15.68±0.77
ICGV 03128 × GPBD 4	20.68±0.33	10.38±0.63	17.50±0.63	18.83±0.43	17.71±0.45
ICGV 03128 × COG 0437	20.68±0.33	25.54±0.39	28.33±0.88	20.80±0.52	20.05±1.19
ICGV 03128 × VRI Gn 6	20.68±0.33	25.41±0.39	26.50±0.76	23.70±0.63	19.00±1.75
Number of primary branches					
CO 7 × GPBD 4	6.25±0.31	7.75±0.48	6.50±0.50	6.22±0.19	7.39±0.45
ICGV 03128 × GPBD 4	5.21±0.22	7.75±0.48	5.40±0.40	3.44±0.11	3.74±0.13
ICGV 03128 × COG 0437	5.21±0.22	5.08±0.29	5.67±0.33	3.90±0.14	3.97±0.26
ICGV 03128 × VRI Gn 6	5.21±0.22	5.00±0.26	5.00±0.58	3.24±0.16	2.38±0.38
Number of pods per plant					
CO 7 × GPBD 4	11.38±0.60	13.00±0.91	14.00±1.00	13.58±0.74	15.32±1.56
ICGV 03128 × GPBD 4	36.21±0.55	13.00±0.91	26.00±0.89	17.43±1.01	17.35±1.24
ICGV 03128 × COG 0437	36.21±0.55	16.08±0.56	45.33±0.88	18.12±1.11	16.72±1.53
ICGV 03128 × VRI Gn 6	36.21±0.55	20.29±0.55	27.00±1.00	14.49±0.96	7.50±0.94
100-pod weight (g)					
CO 7 × GPBD 4	54.86±2.96	65.55±3.61	58.25±4.35	57.26±2.47	44.62±3.88
ICGV 03128 × GPBD 4	105.88±1.87	65.55±3.61	72.36±2.56	75.86±3.02	78.12±3.46
ICGV 03128 × COG 0437	105.88±1.87	47.36±2.31	113.73±4.62	77.54±2.86	69.66±5.75
ICGV 03128 × VRI Gn 6	105.88±1.87	81.82±1.78	95.53±4.52	68.78±3.96	42.44±4.70
100-kernel weight (g)					
CO 7 × GPBD 4	29.55±2.36	29.11±3.47	26.09±3.92	25.99±0.72	18.73±1.23
ICGV 03128 × GPBD 4	37.51±1.51	29.11±3.47	38.78±2.29	31.11±0.92	31.62±1.06
ICGV 03128 × COG 0437	37.51±1.51	20.14±1.70	53.13±3.86	31.78±0.91	28.33±1.79
ICGV 03128 × VRI Gn 6	37.51±1.51	32.37±1.49	32.45±3.57	33.76±1.16	22.33±1.49
Shell weight (g)					
CO 7 × GPBD 4	1.95±0.24	2.55±0.45	0.48±0.26	2.43±0.13	2.77±0.31
ICGV 03128 × GPBD 4	6.48±0.24	2.55±0.45	1.65±0.49	3.70±0.22	3.91±0.26
ICGV 03128 × COG 0437	6.48±0.24	2.36±0.26	5.92±0.47	4.12±0.26	3.61±0.37
ICGV 03128 × VRI Gn 6	6.48±0.24	3.37±0.24	6.17±0.54	2.93±0.23	1.74±0.23
Shelling percentage					
CO 7 × GPBD 4	66.14±0.65	70.22±1.18	69.08±1.49	62.80±0.96	50.87±2.06
ICGV 03128 × GPBD 4	67.61±0.52	70.22±1.18	68.23±0.67	64.27±0.82	62.53±1.16

Cross	P_1	P_2	F_1	F_2	F_3
ICGV 03128 × COG 0437	67.61±0.52	63.42±0.73	64.34±1.38	63.93±0.73	60.62±1.50
ICGV 03128 × VRI Gn 6	67.61±0.52	71.39±0.63	67.84±1.02	66.98±0.85	59.85±2.07
Sound mature kernel (%)					
CO 7 × GPBD 4	88.83±0.97	86.75±1.18	87.50±1.50	91.42±1.63	68.69±4.31
ICGV 03128 × GPBD 4	98.95±0.61	86.75±1.18	80.83±1.23	94.61±1.03	88.03±2.13
ICGV 03128 × COG 0437	98.95±0.61	91.74±0.64	91.67±1.67	95.03±0.97	86.14±3.73
ICGV 03128 × VRI Gn 6	98.95±0.61	98.10±0.64	96.33±1.33	91.17±1.78	95.47±2.29
Pod yield per plant (g)					
CO 7 × GPBD 4	5.97±0.56	9.14±0.96	7.53±1.14	6.96±0.39	6.31±0.82
ICGV 03128 × GPBD 4	23.44±0.40	9.14±0.96	19.05±0.86	11.06±0.67	11.16±0.79
ICGV 03128 × COG 0437	23.44±0.40	6.98±0.53	31.09±0.99	11.86±0.76	9.81±1.18
ICGV 03128 × VRI Gn 6	23.44±0.40	12.19±0.49	19.21±1.23	9.49±0.82	4.32±0.50
Kernel yield per plant (g)					
CO 7 × GPBD 4	4.02±0.52	6.59±0.87	6.25±1.08	4.53±0.28	3.54±0.54
ICGV 03128 × GPBD 4	15.96±0.38	6.59±0.87	10.19±0.71	7.36±0.47	7.24±0.55
ICGV 03128 × COG 0437	15.96±0.38	4.62±0.52	16.51±0.77	7.74±0.52	6.20±0.85
ICGV 03128 × VRI Gn 6	15.96±0.38	8.61±0.42	13.04±1.00	6.57±0.59	2.58±0.31
LLS score					
CO 7 × GPBD 4	4.00±0.33	2.25±0.25	2.65±0.35	3.19±0.13	2.08±0.11
ICGV 03128 × GPBD 4	4.79±0.21	2.25±0.25	2.20±0.20	4.46±0.12	4.54±0.14
ICGV 03128 × COG 0437	4.79±0.21	2.62±0.14	2.67±0.33	4.89±0.09	3.90±0.20
ICGV 03128 × VRI Gn 6	4.79±0.21	3.14±0.21	3.00±0.58	4.52±0.10	4.50±0.19
Rust score					
CO 7 × GPBD 4	4.25±0.25	1.75±0.48	2.33±0.68	4.41±0.16	2.50±0.20
ICGV 03128 × GPBD 4	4.16±0.22	1.75±0.48	1.80±0.37	2.75±0.10	4.06±0.19
ICGV 03128 × COG 0437	4.16±0.22	2.85±0.27	2.50±0.29	1.97±0.12	2.72±0.20
ICGV 03128 × VRI Gn 6	4.16±0.22	3.07±0.27	2.67±0.67	2.16±0.10	3.63±0.42

Scaling test

Scaling test was applied to detect the presence/absence of epistasis. Estimates of scaling test revealed the presence of non-allelic interactions, indicating the inadequacy of additive-dominance model for almost all the characters in most of the crosses except CO 7 × GPBD 4 (number of primary branches, number of pods per plant and pod yield per plant) and ICGV 03128 × GPBD 4 (100-pod weight and shell weight).

Genetic parameters

Gene effects *viz*., mid-parental effect (m), additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) were computed using a five parameter model of generation mean analysis since scaling tests were significant.

Plant height (cm)

The fitting of five-parameter model to the data indicated the involvement of all the three kinds of gene effects *viz*., additive, dominance and epistasis. Additive (d) gene effects were significant in the cross CO 7 × GPBD 4 indicating the involvement of additive gene action in inheritance of plant height and the results are in akin with Shoba *et al.* (2010). All the four types of gene effects were found in the cross ICGV 03128 × GPBD 4 and ICGV 03128

× COG 0437 except dominance (h) and additive × additive (i) gene effects, respectively. Additive (d) and dominance (h) components were significant in the cross ICGV 03128 × VRI Gn 6 but dominance (h) were found to play a major role due to its higher magnitude. The components (h) and (l) observed same sign in ICGV 03128 × COG 0437 exhibiting the presence of complementary epistasis. The presence of additive, dominance and epistatic interactions for this trait were earlier reported by Mothilal (2003).

Number of primary branches

In the cross CO 7 × GPBD 4, the significance in additive (d) and dominance (h) components indicated the involvement of both additive and dominance in control of the number of primary branches. The dominant × dominant (l) interactions were significant and higher in magnitude in the cross ICGV 03128 × GPBD 4 and ICGV 03128 × COG 0437 revealed the greater portion of dominance type of gene effects, while the cross ICGV 03128 × VRI Gn 6 possessed dominance (h) and additive × additive (i) type of gene effects. Similar results were reported by Manivannan *et al.* (2008) and Mothilal and Ezhil (2010).

Number of pods per plant

Simple additive-dominance model were adequate in the cross CO 7 × GPBD 4 since the test for additivity indicated the absence of epistasis. Additive (d), dominance (h) and interaction effects were important in the cross ICGV 03128 × COG 0437 and the signs of dominance (h) and dominance × dominance (l) parameters were same indicated the presence of complementary gene action whereas, the cross ICGV 03128 × GPBD 4 were governed by additive (d) and epistatic interactions for the inheritance of number of pods per plant. The cross ICGV 03128 × VRI Gn 6 expressed additive (d), dominance (h) and additive × additive (i) type of epistatic effects. Shoba *et al.* (2010) noticed the role of additive gene action for this trait.

100-pod weight (g)

Both additive (d) and dominance (h) effects were significant in all the crosses except ICGV 03128 × GPBD 4 in which only additive (d) effects were significant. In almost all the cases, magnitude of dominance (h) were higher than additive (d) indicated the preponderance of dominance gene action for the trait 100-pod weight. The other most prevalent gene effects were the additive × additive (i) type of epistasis. The high dominance × dominance (l) gene effects were recorded by cross CO 7 × GPBD 4. In spite of such higher magnitude, the dominance nature of genes would not be exploited due to the opposite signs of (h) and (l), indicated the presence of duplicate type of epistasis. Manoharan and Thangavelu (2009) and Pavithradevi (2013) opined the participation of additive and non-additive components of gene action for this trait, respectively.

100-kernel weight (g)

The estimates of genetic parameters revealed that the additive (d), dominance (h) and epistatic effects in the cross ICGV 03128 × COG 0437, ICGV 03128 × VRI Gn 6; dominance (h) and epistatic effects in the cross CO 7 × GPBD 4; and additive (d) and dominance × dominance (l) gene effects in the cross ICGV 03128 × GPBD 4 were mainly responsible for the inheritance of 100-kernel weight. Significant value of additive × additive (i) and non-significant value of additive (d) gene effects in the cross CO 7 × GPBD 4 indicated the dispersal of alleles in the parents involved. The additive × additive (i) components were positive and significant in all the crosses except ICGV 03128 × GPBD 4 exhibited that the alleles with positive effects were more often dominant. Further, the (h) and (l) gene effects recorded opposite signs in the cross CO 7 × GPBD 4 and ICGV 03128 × VRI Gn 6 indicated duplicate gene interactions while the same signs in ICGV 03128 × COG 0437 revealed complementary type of epistasis. Role of additive and non-additive gene action for 100-kernel weight were earlier reported by Gaurav *et al.* (2010) and Pavithradevi (2013), respectively.

Shell weight (g)

Additive (d), dominance (h) and additive × additive (i) type of epistatic effects were important in the crosses *viz.*, ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6 while the dominance (h) gene effects governed the inheritance of shell weight in CO 7 × GPBD 4. Both additive (d) and dominance (h) gene effects were found to be significant in the cross ICGV 03128 × GPBD 4 in which additive (d) gene effects registered higher magnitude for shell weight. The component additive × additive (i) were positive and significant in ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6 which indicated that alleles with positive effects are more often dominant.

Shelling percentage

In two crosses *viz*., CO 7 × GPBD 4 and ICGV 03128 × VRI Gn 6, the gene effects (d), (h), (i) and (l) were significant indicated the involvement of additive, dominance and other epistatic interactions, and the components (h) and (l) had opposite signs revealed the existence of duplicate epistasis in the inheritance of shelling percentage. Additive (d) and dominance (h) gene effects along with additive × additive (i) interactions were found to be significant in the cross ICGV 03128 × COG 0437 while, additive (d) and dominance (h) were significant in ICGV 03128 × GPBD 4. The greater magnitude of dominance than additive in all the crosses revealed the predominance of dominance gene action for this trait. Similar results were reported by Parameshwarappa and Girishkumar (2007) for the trait shelling percentage.

Sound mature kernel (%)

The genetic parameters (d), (h), (i) and (l) were significant in the cross ICGV 03128 × COG 0437 indicated the involvement of additive, dominance and other epistatic interactions for sound mature kernel per cent. The presence of dominance (h), additive × additive (i) and dominance × dominance (l) gene effects were observed in the cross CO 7 × GPBD 4 whereas, the cross ICGV 03128 × GPBD 4 possessed the additive (d), interaction (i) and (l) effects. Contrary to the present results, Hariprasanna *et al*. (2008) reported additive effects for this character. On the other hand, Jivani *et al.* (2009), Ganesan *et al.* (2010) and Savithramma *et al*. (2010) reported the involvement of non-additive gene action for this trait. The crosses *viz.*, CO 7 × GPBD 4 and ICGV 03128 × COG 0437 exhibited duplicate type of epistasis for sound mature kernel per cent.

Pod yield per plant (g)

Considering the pod yield per plant, additive (d), dominance (h) and inter-allelic interaction effects (i) and (l) were equally important in the crosses *viz.*, ICGV 03128 × GPBD 4 and ICGV 03128 × COG 0437. Additive (d) gene effects were responsible for the expression of pod yield in CO 7 × GPBD 4 while (d), (h) and (i) effects were significant in ICGV 03128 × VRI Gn 6 indicated the involvement of additive, dominance and additive × additive type of epistatic interactions. The same signs of (h) and (l) in ICGV 03128 × GPBD 4 and ICGV 03128 × COG 0437 revealed the preponderance of complementary epistasis. Gaurav *et al.* (2010) and Shoba *et al.* (2010) reported additive gene action to be involved in the inheritance of this trait. However, non-additive gene action holds good for this trait were reported by Mothilal and Ezhil (2010), Savithramma *et al*. (2010), Pavithradevi (2013) and Azad *et al.* (2014).

Kernel yield per plant (g)

Regarding the kernel yield per plant, additive (d), dominance (h) and epistatic gene effects (i) and (l) were important in the cross ICGV 03128 × COG 0437 whereas, additive (d), dominance (h) and additive × additive (i) type of gene effects were mainly responsible for the expression of this character in ICGV 03128 × VRI Gn 6. Additive (d) and dominance (h) gene effects were expressed in the cross CO 7 × GPBD 4. The significance of (d) and (i) effects in ICGV 03128 × GPBD 4 suggested the possible role of additive (d), additive × additive (i) type of gene effect in the inheritance of this trait. Predominance of complementary type of epistasis was noticed in the cross ICGV 03128 × COG 0437. The present findings are in close agreement with the results obtained by Savithramma *et al*. (2010) and Pavithradevi (2013). Contrary to the present results, Shoba *et al.* (2010) and Vishnuvardhan *et al.* (2014) reported additive gene action for this trait.

Late leaf spot score

The crosses *viz.*, CO 7 × GPBD 4 and ICGV 03128 × GPBD 4 showed additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) interactions. Apart from additive (d) gene effects, two types of epistatic interactions *viz.*, additive × additive (i) and dominance × dominance (l) were controlling the trait in ICGV 03128 × COG 0437 and ICGV 03128 × VRI Gn 6. In case of interaction effects, the magnitudes of component (i) were higher than (l) implied the importance of additivity in all the four crosses. A duplicate type of non-allelic interaction were involved in the cross CO 7 × GPBD

4 due to the opposite signs of (h) and (l), whereas same signs in ICGV 03128 × GPBD 4 revealed complementary type of epistasis in inheritance of this trait. Vishnuvardhan *et al.* (2014) noticed additive gene effects while Vishnuvardhan *et al.* (2011) observed non additive gene effects operating for the trait late leaf spot.

Rust score

Additive (d) and dominance (h) gene effects along with additive × additive (i) and dominance × dominance (l) interactions were significant in the cross CO 7 × GPBD 4 while the other three crosses exhibited additive (d), dominance (h) and dominance × dominance (l) gene effects for the trait rust score. The opposite signs of the components (h) and (l) showed the duplicate type of epistasis in all the crosses. The component (i) was positive and significant in CO 7 × GPBD 4 which implied alleles with positive effects were dominant. Additive gene effects were earlier observed by Vishnuvardhan *et al.* (2014) while non additive gene effects were reported by Shoba *et al.* (2010) and Vishnuvardhan *et al.* (2011) for this trait.

Table 2: Scaling test and estimates of genetic parameters for various vegetative and reproductive characters in groundnut

Cross	Scales		Parameters				
	C	D	m	d	h	i	l
Plant height (cm)							
CO 7 × GPBD 4	16.12**±2.71	9.59**±3.31	15.32**±0.44	0.88*±0.37	-3.62±2.34	-1.96±2.03	-8.71±6.01
ICGV 03128 × GPBD 4	9.27**±2.26	2.11±2.13	18.83**±0.43	5.15**±0.35	2.11±1.54	10.45**±1.52	-9.54*±4.55
ICGV 03128 × COG 0437	-19.68**±2.77	-7.62±4.90	20.80**±0.52	-2.43**±0.25	7.02*±3.39	-3.05±2.69	16.07*±7.94
ICGV 03128 × VRI Gn 6	-4.28±2.98	-17.51*±7.14	23.70**±0.63	-2.37**±0.26	14.41**±4.87	6.23±3.71	-17.63±10.80
Number of primary branches							
CO 7 × GPBD 4	-2.14±1.38	3.15±1.93	6.22**±0.19	-0.75**±0.29	-2.95*±1.31	-	-
ICGV 03128 × GPBD 4	-10.01**±1.06	-4.88**±0.78	3.44**±0.11	-1.27**±0.26	0.51±0.49	-0.95±0.59	6.83**±1.57
ICGV 03128 × COG 0437	-6.00**±0.95	-2.23*±1.14	3.90**±0.14	0.07±0.18	1.01±0.78	0.62±0.71	5.03*±2.00
ICGV 03128 × VRI Gn 6	-7.25**±1.37	-7.19**±1.57	3.24**±0.16	0.11±0.17	3.48**±1.12	3.80**±0.96	0.07±2.83
Number of pods per plant							
CO 7 × GPBD 4	1.93±3.75	9.74±6.52	13.58**±0.74	-0.81±0.55	-4.36±4.48	-	-
ICGV 03128 × GPBD 4	-31.50**±4.55	-14.65**±5.47	17.43**±1.01	11.61**±0.53	5.91±3.92	27.73**±3.56	22.46*±10.72
ICGV 03128 × COG 0437	-70.49**±4.85	-21.62**±6.58	18.12**±1.11	10.07**±0.39	21.86**±4.69	22.80**±4.08	65.15**±12.31
ICGV 03128 × VRI Gn 6	-52.52**±4.39	-55.48**±4.31	14.49**±0.96	7.96**±0.39	26.99**±3.23	44.16**±3.11	-3.95±9.55
100-pod weight (g)							
CO 7 × GPBD 4	-7.87±13.96	-56.46**±16.94	57.26**±2.47	-5.34*±2.33	34.37**±11.82	25.64*±10.71	-64.78*±30.85
ICGV 03128 × GPBD 4	-12.71±13.72	-10.68±15.65	75.86**±3.02	20.17**±2.04	-8.36±11.16	-	-
ICGV 03128 × COG 0437	-70.55**±14.99	-29.68±23.87	77.54**±2.86	29.26**±1.49	45.14**±16.64	66.55**±13.56	54.50±40.16

ICGV 03128 × VRI Gn 6	-103.67**±18.42	-155.51**±20.57	68.78**±3.96	12.03**±1.29	88.07**±15.13	110.46**±13.76	-69.12±42.17
100-kernel weight (g)							
CO 7 × GPBD 4	-6.88±9.34	-35.74**±6.62	25.99**±0.72	0.22±2.10	19.43**±4.43	23.12**±5.19	-38.47**±13.61
ICGV 03128 × GPBD 4	-19.76**±6.98	-2.33±5.96	31.11**±0.92	4.20*±1.89	3.74±3.69	6.66±4.22	23.23*±11.08
ICGV 03128 × COG 0437	-36.79**±8.85	-7.89±7.72	31.78**±0.91	8.68**±1.14	23.43**±5.72	16.49**±5.31	38.54*±15.83
ICGV 03128 × VRI Gn 6	0.28±8.76	-48.06**±6.74	33.76**±1.16	2.57*±1.06	29.60**±5.18	37.23**±5.14	-64.46**±15.46
Shell weight (g)							
CO 7 × GPBD 4	4.27**±0.90	1.73±1.38	2.43**±0.13	-0.30±0.26	-2.22*±0.90	-1.04±0.79	-3.39±2.10
ICGV 03128 × GPBD 4	2.45±1.41	-0.77±1.25	3.70**±0.22	1.96**±0.25	-1.94*±0.89	-	-
ICGV 03128 × COG 0437	-4.20**±1.44	-2.64±1.60	4.12**±0.26	2.06**±0.18	2.55*±1.15	5.18**±1.04	2.08±3.11
ICGV 03128 × VRI Gn 6	-10.49**±1.46	-8.76**±1.08	2.93**±0.23	1.56**±0.17	5.33**±0.85	7.20**±0.87	2.31±2.64

Cross	Scales		Parameters				
	C	D	m	d	h	i	l
Shelling percentage							
CO 7 × GPBD 4	-23.29**±5.04	-58.50**±8.56	62.80**±0.96	-2.04**±0.67	36.01**±5.90	31.04**±4.76	-46.94**±13.97
ICGV 03128 × GPBD 4	-17.22**±3.75	-16.24**±5.09	64.27**±0.82	-1.31*±0.64	7.27*±3.53	5.34±3.12	1.31±9.17
ICGV 03128 × COG 0437	-4.00±4.12	-16.40**±6.24	63.93**±0.73	2.10**±0.44	9.10*±4.36	14.46**±3.57	-16.53±10.57
ICGV 03128 × VRI Gn 6	-6.77±4.05	-33.56**±8.50	66.98**±0.85	-1.89**±0.41	19.59**±5.82	17.46**±4.54	-35.72**±13.27
Sound mature kernel (%)							
CO 7 × GPBD 4	15.11*±7.35	-83.68**±17.61	91.42**±1.63	1.04±0.76	58.02**±11.99	60.39**±9.21	-131.73**±26.74
ICGV 03128 × GPBD 4	31.07**±4.98	-22.78**±8.86	94.61**±1.03	6.10**±0.67	8.35±6.10	32.56**±4.91	-71.80**±14.41
ICGV 03128 × COG 0437	6.09±5.19	-36.19*±15.07	95.03**±0.97	3.61**±0.44	21.46*±10.20	32.35**±7.56	-56.37**±21.81
ICGV 03128 × VRI Gn 6	-25.04**±7.65	2.51±9.86	91.17**±1.78	0.43±0.44	-8.03±7.12	-4.99±6.26	36.73±19.07
Pod yield per plant (g)							
CO 7 × GPBD 4	-2.31±2.98	-3.78±3.54	6.96**±0.39	-1.59**±0.55	2.11±2.44	-	-
ICGV 03128 × GPBD 4	-26.43**±3.35	-10.06**±3.58	11.06**±0.67	7.15**±0.52	5.06*±2.56	16.60**±2.40	21.83**±7.18
ICGV 03128 × COG 0437	-45.16**±3.70	-14.92**±4.99	11.86**±0.76	8.23**±0.33	18.30**±3.55	18.87**±3.04	40.32**±9.15
ICGV 03128 × VRI Gn 6	-36.09**±4.13	-37.35**±2.66	9.49**±0.82	5.62**±0.32	20.29**±2.26	30.13**±2.45	-1.68±7.78

Kernel yield per plant (g)							
CO 7 × GPBD 4	-4.98±2.63	-5.50*±2.46	4.53**±0.28	-1.29*±0.51	3.79*±1.71	0.27±1.64	-0.70±4.64
ICGV 03128 × GPBD 4	-13.48**±2.54	-8.29**±2.58	7.36**±0.47	4.69**±0.48	2.20±1.81	12.65**±1.75	6.93±5.13
ICGV 03128 × COG 0437	-22.63**±2.68	-11.28**±3.60	7.74**±0.52	5.67**±0.33	9.97**±2.54	15.08**±2.18	15.13*±6.48
ICGV 03128 × VRI Gn 6	-24.39**±3.15	-27.38**±1.82	6.57**±0.59	3.67**±0.28	14.95**±1.60	21.54**±1.80	-3.99±5.69
LLS score							
CO 7 × GPBD 4	1.21±0.96	-4.31**±0.65	3.19**±0.13	0.88**±0.21	2.60**±0.45	4.83**±0.60	-7.36**±1.49
ICGV 03128 × GPBD 4	6.39**±0.70	2.20**±0.69	4.46**±0.12	1.27**±0.16	-1.72**±0.46	2.14**±0.50	-5.59**±1.32
ICGV 03128 × COG 0437	6.84**±0.80	-1.61±0.86	4.89**±0.09	1.09**±0.13	1.17±0.61	4.38**±0.56	-11.26**±1.57
ICGV 03128 × VRI Gn 6	4.14**±1.25	1.03±0.83	4.52**±0.10	0.82**±0.15	-0.97±0.66	1.65*±0.66	-4.14*±1.99
Rust score							
CO 7 × GPBD 4	6.97**±1.58	-4.81**±1.02	4.41**±0.16	1.25**±0.27	3.69**±0.77	6.87**±0.82	-15.71**±2.44
ICGV 03128 × GPBD 4	1.50±1.00	4.83**±0.96	2.75**±0.10	1.20**±0.26	-4.13**±0.61	-0.56±0.62	4.44**±1.65
ICGV 03128 × COG 0437	-4.13**±0.82	-0.04±0.90	1.97**±0.12	0.66**±0.18	-1.66**±0.61	0.65±0.59	5.45**±1.61
ICGV 03128 × VRI Gn 6	-3.92**±1.43	2.95±1.73	2.16**±0.10	0.54**±0.17	-3.57**±1.22	-1.53±1.00	9.16**±2.96

***, ** Significant @ 5% and 1% level of probability, respectively.**

Table 3. Exploitation of desirable crosses through pedigree method of breeding in groundnut

S.No.	Characters	Desirable Crosses	Gene Action
1	Plant height (cm)	CO 7 × GPBD 4	Additive gene effects
		ICGV 03128 × COG 0437	Complementary epistasis
2	Number of primary branches	-	-
3	Number of pods per plant	ICGV 03128 × COG 0437	Complementary epistasis
4	100-pod weight (g)	ICGV 03128 × GPBD 4	Additive gene effects
5	100-kernel weight (g)	ICGV 03128 × COG 0437	Complementary epistasis
6	Shell weight (g)	-	-
7	Shelling percentage	-	-
8	SMK (%)	-	-
9	Pod yield per plant (g)	CO 7 × GPBD 4	Additive gene effects
		ICGV 03128 × GPBD 4	Complementary epistasis
		ICGV 03128 × COG 0437	Complementary epistasis
10	Kernel yield per plant (g)	ICGV 03128 × GPBD 4	Additive & additive × additive gene effects
		ICGV 03128 × COG 0437	Complementary epistasis
11	LLS score	ICGV 03128 × GPBD 4	Complementary epistasis
12	Rust score	-	-

Inferences based on the magnitudes of additive effects are not advisable, because the distribution of positive and negative gene effects in the parents may result in different degrees of cancellation of effects in the expression and thereby do not necessarily reflect in the magnitude of additive variance. However, dominance (h) and dominance × dominance (l) are independent of the degree of gene distribution due to which their combined estimates could be considered to be the best representative. So, practically these are the only components which can safely be used to determine the type of epistasis which may have influence on the observed performance of generations Mather and Jinks 1982. For the same reason, emphasis has been given to the characters which are governed by such gene effects for suggesting appropriate breeding method that should be followed to achieve higher expression of such characters.

The presence of duplicate epistasis would be detrimental for rapid progress, making it difficult to fix genotypes with increased level of character manifestation because the positive effects of one parameter would be cancelled out by the negative effects of another. Hence, early generation intermating besides accumulating the favorable genes and maintaining heterozygosity in the population is likely to throw useful recombinants (Shoba *et al.*, 2010). Complementary epistasis helps in effective execution of pedigree breeding. Based on the criteria mentioned above, the possible exploitation of desirable crosses through pedigree breeding is presented in Table 3.

Conclusion

The characters governed by additive (d) gene effects and additive × additive (i) gene interaction effects are fixable. Also, the crosses which are governed by complementary epistasis where signs of dominance (h) gene effects and dominance × dominance (l) gene interaction effects are similar are also worth exploitation. Such crosses have the potentiality to produce transgressive segregants on the positive side. Pedigree method of breeding followed by simple selection in later segregating generations will be a meaningful breeding strategy to be followed in such crosses for the improvement of the characters under consideration. The generation mean analysis of this study brought out the genetics of yield and its components in each of the four cross combinations studied in detail. From the foregoing discussion, it may be concluded that in all the vegetative and reproductive characters, additivity, dominance and one or more of the epistatic effects determined the expression. Considering the kernel yield per plant, pod yield per plant and foliar disease incidence, the cross ICGV 03128 × GPBD 4 was judged as the best cross for further selection programme.

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