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## Genetics of late leaf spot disease resistance and pod productivity *per se* traits in two interspecific crosses of groundnut (*Arachis hypogaea* L.)

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### Abstract

To study the genetic basis of late leaf spot (LLS) disease, pod yield and yield attributing characters in groundnut crosses GKVK 17 × ICGV 86590 and GPBD 4 × TMV 2 was developed using contrasting parents for LLS disease and yield attributing traits. The material for present investigation consisted of five generations P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> of two crosses. Observations were recorded on growth parameters and LLS disease scores of P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> progenies at 60<sup>th</sup>, 75<sup>th</sup>, 90<sup>th</sup> and 115<sup>th</sup> DAS. Test of segregation of F<sub>2</sub> individuals for LLS disease resistance showed significant difference when tested for Mendelian ratios, indicated that LLS disease is governed by interaction of genes. In all the vegetative and reproductive characters, additive, dominance and one or more of the epistatic effects determined the expression. Therefore, individual plant selection could be appropriate for improvement of yield *per se* traits and LLS disease. There are 76 superior segregates in GKVK 17 × ICGV 86590 and 65 superior segregates in GPBD 4 × TMV 2 with lower LLS disease score coupled with higher pod yield would be selected.

**Keywords:** leaf spot disease, pod productivity *per se* traits, groundnut

### Introduction

Groundnut (*Arachis hypogaea* L.) is an important oil seed crop of the world, having originated from Brazil in South America and is presently cultivated throughout tropical, subtropical and warm temperate regions of the world. International Crops Research Institute for Semi-Arid Tropics (ICRISAT) and the United Nations Food and Agricultural Organization (UN-FAO) identified it as the third most important source of vegetable protein, fourth most important source of vegetable oil, and twelfth most important food crop.

Groundnut is cultivated in around 100 countries located between 40°N to 40°S with a world production of 34.9 million tonnes from an area of 23.4 million hectares with a productivity of 1490 kg per hectare. India shares 22 *per cent* of the world groundnut production and grown in about 4.59 million hectares with a production of 8.05 million tonnes and productivity of 1552 kg per hectare (2016-17 Indiastat.com). The principal groundnut producing states of India are Gujarat, Andhra Pradesh, Tamil Nadu, Karnataka, and Maharashtra which accounts for more than 80 *per cent* of all India production as well as area. In Karnataka it is grown in an area of about 4.7 lakh ha with the production of 5.6 lakh tonnes and productivity of 769 kg/ha (2015-16 Indiastat.com).

Foliar fungal diseases are the major production constraints of groundnut crop globally of these, late leaf spot (LLS) caused by *Phaeoisariopsis personata* (Berk. & M.A. Curtis) is a major and widely distributed disease. It can cause total defoliation and reduce pod and fodder yields to an extent of over 50 *per cent* and adversely affect the quality of its pods (Subrahmanyam *et al.* 1984; Waliyar 1993). Chemical control measures are available but they increase production cost by 10 *per cent* (Coffelt and Porter, 1986) and are beyond reach of small and marginal farmers, who are the major producers of this crop. Therefore, development and adoption of resistant cultivars is the best option to minimize loss at farm level and maintain good product quality (Dwivedi *et al.*, 1993).

Keeping these points in view, an attempt has been made to study the genetic basis of late leaf spot disease, Pod yield and its attributing characters and their interrelations in groundnut with the following objective to estimate mode of action of genes controlling resistance to late leaf spot disease, pod yield and its component traits.

### Material and method

Five generations P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations of the two crosses *i.e.*, GPBD 4 × TMV 2,

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GKVK 17 × ICGV 86590 were evaluated in disease control and disease stress condition separately. Non-segregating generations *viz.*, P<sub>1</sub>, P<sub>2</sub> and F<sub>1</sub> were grown with two replications. Whereas segregating generations *viz.*, F<sub>2</sub> plants were grown in a separate contiguous block and F<sub>3</sub> progeny families were grown in augmented design, each family consisted of 10 to 12 plants with a spacing of 30 × 20 cm in eight blocks without replication. Observations to be recorded on following growth and yield parameters *viz.*, Days to flowering, Plant height (cm), Primary branches per plant, Pods per plant, Kernel per plant, Pod yield per plant (g), Kernel yield per plant (g), Shelling percentage, Sound mature kernel percentage, 100 kernel weight (g)

All the genotypes were evaluated for late leaf spot disease (*kharif* 2016) through visual screening method (Fig. 1) using modified 9 point scale for late leaf spot disease given by Subrahmanyam *et al.* in 1995. The scores were converted into Percentage Disease Index (PDI). They were also evaluated for

yield and yield attributing traits.

#### Scoring for late leaf spot disease

Visual screening (Fig 1) with modified 9 point scale as given by Subrahmanyam *et al.*, 1995 was used for screening genotypes for late leaf spot disease under disease stress condition experiment as mentioned under Table 1. The visual scores (1-9) and extent of leaf area destroyed (0-100%) are linearly related to each other. The field disease scores were mainly based on the extent of leaf area damage. Scoring of disease was done at 65<sup>th</sup>, 75<sup>th</sup>, 90<sup>th</sup> and 115<sup>th</sup> days after sowing (DAS) in all the five generations.

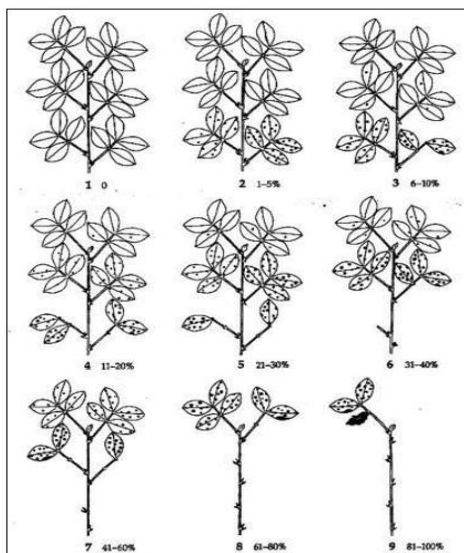
The scores were converted into percentage disease index (PDI) by using the following formula.

$$\text{PDI (\%)} = \frac{\text{Sum of individual rating}}{\text{Number of observations assessed}} \times \frac{100}{\text{Maximum disease rating}}$$

**Table 1:** Modified 9-point scale for field evaluation of late leaf spot disease in Groundnut

Sl. No	Disease score	Disease severity (%)*
1	No disease	0
2	Lesions present largely on lower leaves, no defoliation	1-5
3	Lesions present largely on lower leaves, very few on middle leaves; defoliation of some leaflets evident on lower leaves	6-10
4	Lesions present on lower and middle leaves but severe on lower leaves, defoliation of some leaflets evident on lower leaves	11-20
5	Lesions present on lower and middle leaves, over 50 % of defoliation of lower leaves	21-30
6	Severe lesions on lower and middle leaves; lesions present but less severe on top leaves; extensive defoliation of lower leaves; some defoliation on middle leaves	31-40
7	Lesions on all leaves but less severe on top leaves; defoliation of all lower and middle leaves	41-60
8	Defoliation of all lower and middle leaves; severe lesions on top leaves evident	61-80
9	Almost all leaves defoliated, leaving bare stem; some leaflets may remain, but show severe leaf spot	81-100

\*percentage leaf area damaged by late leaf spot



**Fig 1:** Diagram showing leaf symptoms used for scoring late leaf spot disease resistance (Subrahmanyam *et al.*, 1990)

#### Results

The present investigation was undertaken to estimate mode of action of genes controlling resistance to late leaf spot disease, pod yield and its component traits. Hybridization was carried out to generate hybrids and evaluation of F<sub>2</sub> generation of two crosses GPBD 4 × TMV 2 and GKVK 17 × ICGV 86590 was undertaken during summer 2016. During *kharif*-2016 five generations P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> of the four crosses were

evaluated in disease control and disease stress condition separately.

#### Gene action for LLS disease and pod yield and yield attributes by generation mean analysis *er se* performance of parents, F<sub>1</sub>'s and segregating generations

The mean of both non-segregating (P<sub>1</sub>, P<sub>2</sub> and F<sub>1</sub>) and segregating generations (F<sub>2</sub> and F<sub>3</sub>) of two crosses were higher for traits like pods per plant, pod yield per plant, kernel yield per plant, sound mature kernel percentage and shelling percentage. Mean values of all the five generations for all the traits were comparable between GPBD 4 × TMV 2 and GKVK 17 × ICGV 86590. F<sub>1</sub> trait means of the crosses were intermediate for days to first flowering, plant height, primary branches per plant and LLS disease. Whereas, means of F<sub>1</sub> traits were slightly higher for pods per plant, pod yield per plant, kernel yield per plant and SMK (%) than their respective parents. The means of F<sub>2</sub> and F<sub>3</sub> generation were higher than those of F<sub>1</sub>'s for pods per plant, kernel yield per plant whereas lower means were noticed for PDI @ 65<sup>th</sup> DAS, PDI @ 75<sup>th</sup> DAS, PDI @ 90<sup>th</sup> DAS and PDI @ 115<sup>th</sup> DAS (Table 2 and 2a )

#### Joint scaling test

The significance of joint-scaling test indicated inadequacy of additive-dominance model for the expression of pod yield and its attributing traits (Table 3).

### Estimates of gene effects for pod yield and its attributing traits

After ascertaining the failure of additive-dominance model in explaining the inheritance of various quantitative traits, perfect fit solution (Jinks and Jones, 1958) was fitted to estimate the magnitude and direction of the di-genic interaction effects for four crosses and the results (Table 3a) of which are presented below character wise. The mid-parent effect (m) was significant and positive for all the crosses.

#### Days to first flowering

Dominance (h) and Dominance  $\times$  dominance (l) components were significant in the cross GPBD 4  $\times$  TMV 2. Both Additive  $\times$  additive (i) and dominance  $\times$  dominance (l) were significant in the cross GKVK 17  $\times$  ICGV 86590 but dominance  $\times$  dominance (l) play a major role due to its higher magnitude. The components (h) and (l) observed opposite sign in both the crosses exhibiting the presence of duplicate epistasis.

#### Plant height (cm)

Significant additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were significant in GKVK 17  $\times$  ICGV 86590 while the dominance (h) gene effect, additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects was important in GPBD 4  $\times$  TMV 2. The components (h) and (l) observed opposite signs in all the crosses exhibiting the presence of duplicate epistasis.

#### Primary branches per plant

Dominance  $\times$  dominance (l) type of epistatic effect was important in GPBD 4  $\times$  TMV 2. While, Dominance (h) and dominance  $\times$  dominance (l) components were significant in the cross GKVK 17  $\times$  ICGV 86590 indicated that dominant gene effect and dominant epistatic effect plays major role in the inheritance of this trait. The components (h) and (l) observed opposite sign in all the crosses exhibiting the presence of duplicate epistasis.

#### Pods per plant (g)

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects was important in both the crosses. The components (h) and (l) observed opposite sign in all the crosses exhibiting the presence of duplicate epistasis.

#### Pod yield per plant (g)

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were found to be significant in the cross GPBD 4  $\times$  TMV 2 while the dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were important in the cross GKVK 17  $\times$  ICGV 86590 for the inheritance of this trait. The components (h) and (l) observed opposite signs in both crosses exhibiting the presence of duplicate epistasis.

#### Kernel yield per plant (g)

Dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects governed the inheritance of kernel yield of both the crosses. The components (h) and (l) observed opposite signs in both the crosses exhibiting the presence of duplicate epistasis.

### Shelling percentage

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were significant and the components (h) and (l) showed similar signs in both the crosses exhibiting the presence of complementary epistasis.

#### Sound mature kernel percentage

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects are observed and components (h) and (l) observed opposite signs in both crosses exhibiting the presence of duplicate epistasis.

### Test of segregation ratio of F<sub>2</sub> individuals for late leaf spot resistance

Results obtained from the analysis of di-genic inheritance of late leaf spot disease resistance using  $\chi^2$  test among F<sub>2</sub> population in the four crosses are presented in Table 4.

F<sub>2</sub> individuals were tested for the expected ratio of 9R: 3MR: 3MS: 1S in four crosses. Among 100 F<sub>2</sub> plants derived from GPBD 4  $\times$  TMV 2, 80 F<sub>2</sub> plants showed resistance (R), 10 plants exhibited moderate resistance (MR), 4 showed moderate susceptibility (MS) and 6 F<sub>2</sub> plants showed susceptible reaction with significant  $\chi^2$  value 14.62 in the cross GPBD 4  $\times$  TMV 2. However, 77 F<sub>2</sub> plants noticed resistance (R), 14 plants exhibited moderately resistance (MR), 2 plants showed moderately susceptibility (MS) and 7 F<sub>2</sub> plants showed susceptible reaction with significant  $\chi^2$  value 12.45 in GKVK 17  $\times$  ICGV 86590 (Table 4).

Further, both the four crosses were tested for the expected ratio of 15R: 1S which is presented in Table 4a. Both crosses GPBD 4  $\times$  TMV 2, GKVK 17  $\times$  ICGV 86590 exhibited non-significant to  $\chi^2$  test when tested against 15R:1S. Similar results also found when we observed disease severity of each family in F<sub>3</sub> generation. Each family further categorized into R, MR, MS and S based on PDI. Both crosses exhibited different ratios not specific to Mendelian ratios, LLS disease reaction in F<sub>3</sub> families of four crosses was presented in Table 4b. After test of significant segregation pattern of F<sub>2</sub> and F<sub>3</sub> generation, gene effects of LLS disease was estimated.

#### Joint scaling test for late leaf spot disease

The significance of joint-scaling test indicated inadequacy of additive-dominance model for the expression of LLS disease (Table 5)

### Estimates of gene effects for LLS disease reaction

#### PDI @ 65<sup>th</sup> DAS

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were important in the cross GKVK 17  $\times$  ICGV 86590 while the dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were important in the crosses *viz.*, GPBD 4  $\times$  TMV 2. The components (h) and (l) observed opposite sign in both crosses exhibiting the presence of duplicate epistasis (Table 6).

#### PDI @ 75<sup>th</sup> DAS

Additive (d), dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were important in the cross and GKVK 17  $\times$  ICGV 86590 while the dominance (h), additive  $\times$  additive (i) and dominance  $\times$  dominance (l) type of epistatic effects were important in the cross GPBD 4  $\times$  TMV 2. The components (h) and (l) observed opposite sign in both the crosses exhibiting the

presence of duplicate epistasis.

#### **PDI @ 90<sup>th</sup> DAS and PDI @ 115<sup>th</sup> DAS**

Additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) type of epistatic effects were important in both the crosses and the components (h) and (l) observed opposite sign in both the crosses exhibiting the presence of duplicate epistasis for PDI @ 90<sup>th</sup> DAS and PDI @ 115<sup>th</sup> DAS.

#### **Discussion**

##### **Gene action for pod yield and yield attributes by generation mean analysis**

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 mean analysis with first degree statistics was adopted to detect non-allelic interaction component of the mean of the phenotypic distribution.

Five generation mean analysis of four crosses was conducted to estimate and test the significance of epistatic gene effects in the present investigation.

##### **Joint scaling tests**

A perusal of the Table 4 clearly indicated the inadequacy of additive-dominance model for the expression of pod yield per plant and its component traits and LLS disease in all the four crosses. As evident from highly significant Cavalli's joint scaling test. The inadequacy of additive-dominance model necessitated to include digenic epistatic gene interaction to explain the observed variation in generation means for various quantitative characters. The inadequacy of additive-dominance model for pod yield and its component traits was earlier reported by Prabhu *et al.* (2016).

##### **Estimates of gene effects for pod yield and its attributing traits**

After ascertaining the failure of additive-dominance model, perfect fit solution (Jinks and Jones, 1958) was fitted to estimate the magnitude and direction of the digenic interaction effects for the two crosses, the results of the same are summarized in Table 5.

Predominance of dominance gene effect and higher magnitude of dominance epistatic gene effects for days to first flowering, plant height, primary branches per plant, pods per plant, pod yield per plant, kernel yield per plant, shelling percentage and SMK (%) was observed compared to other gene effects in both the crosses. However, additive × additive gene effects also played an important role for the expression of plant height, pods per plant, pod yield per plant, kernel yield per plant, shelling percentage and SMK (%) in both crosses. The signs indicate the direction in which a particular gene action is ultimately acting. For days to first flowering, pods per plant, pod yield per plant and kernel yield per plant, dominant × dominant gene action with negative sign in both the crosses was observed with duplicate epistasis which tends to reduce the trait expression and the genetic gain is faster with mild selection and less rapid with very intense selection. 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 effect of one parameter would be cancelled out by the negative effect 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 type of epistasis was observed for shelling percentage in GPBD 4 × TMV 2. Complementary epistasis helps ineffective execution of pedigree breeding. The present findings are in close agreement with the results obtained by Manivannan *et al.* (2008), Mothilal and Ezhil (2010), Savithamma *et al.* (2010), Jivani *et al.* (2009), Pavithradevi (2013). Venkateswarlu *et al.* (2007) reported additive and non-additive gene action for these traits.

##### **Test of segregation ratio of F<sub>2</sub> individuals for late leaf spot resistance**

Results obtained from the analysis of inheritance of late leaf spot disease resistance using  $\chi^2$  test among F<sub>2</sub> plants derived from both the crosses showed significance for  $\chi^2$  value against the expected ratio of 9R: 3MR: 3MS: 1S (Table 6) indicating that inheritance of late leaf spot disease genes are not governed by two genes. GPBD 4 × TMV 2 and GKVK 17 × ICGV 86590 crosses indicated that consistent 15R: 1S ratio, when tested against expected 15R: 1S ratio with non-significant  $\chi^2$  value implies that LLS disease in these crosses is controlled by two genes with interaction effect.

##### **Estimates of gene effects for late leaf spot disease**

Predominance of dominance gene effect and additive and dominance epistatic gene effects was observed for PDI @ 65<sup>th</sup>, PDI @ 75<sup>th</sup>, PDI @ 90<sup>th</sup> and PDI @ 115<sup>th</sup> DAS indicated that involvement of both additive and dominance epistatic interactions in the inheritance of LLS disease in both crosses. Vishnuvardhan *et al.* (2014) noticed additive gene effects while Vishnuvardhan *et al.* (2011) observed non-additive gene effects operating for the late leaf spot.

Inferences based on the magnitude 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 might have influenced 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 suggesting appropriate breeding method that should be followed to achieve higher expression of such characters.

All other characters including the foliar disease incidence had epistatic gene action which included additive as well as dominance type gene interaction, especially pod yield component traits and LLS disease incidence in four crosses implies selection should be postponed to later generations.

**Table 2:** Mean and standard error of various generations for pod yield component traits in Groundnut

Traits	P <sub>1</sub>	P <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	F <sub>3</sub>
<b>Days to first flowering</b>					
GPBD 4 × TMV 2	30.20±0.20	30.80±0.37	32.40 ± 0.92	38.24±0.42	33.69 ± 0.09
GKVK 17 × ICGV 86590	30.80±0.37	30.80 ± 0.37	31.20±0.37	35.21±0.44	33.60±0.04
<b>Plant height (cm)</b>					
GPBD 4 × TMV 2	16.60±0.24	18.60±0.60	20.80±0.37	15.97±0.44	31.30±0.19
GKVK 17 × ICGV 86590	34.40±0.67	19.04 ± 0.31	21.80 ± 0.37	21.47 ± 0.42	42.42 ± 0.81
<b>Primary branches/plant</b>					
GPBD 4 × TMV 2	2.40±0.24	2.80±0.20	3.60±0.24	6.26±0.12	5.01±0.06
GKVK 17 × ICGV 86590	3.54±0.06	2.94±0.04	4.12±0.36	7.19±0.11	5.69±0.04
<b>Pods/plant (g)</b>					
GPBD 4 × TMV 2	24.00±0.44	20.0±4.50	25.60±0.24	42.78±1.75	20.56±0.84
GKVK 17 × ICGV 86590	18.80±0.58	19.82±0.33	28.60±0.33	48.72±1.45	17.21±0.53
<b>Pod yield /plant (g)</b>					
GPBD 4 × TMV 2	12.56±0.21	7.00 ± 0.44	18.20 ± 0.20	26.22 ± 1.19	17.36 ± 0.85
GKVK 17 × ICGV 86590	13.60±1.02	14.30±0.37	15.90±0.48	36.20±1.17	14.09±0.51
<b>Kernel yield/plant (g)</b>					
GPBD 4 × TMV 2	7.89±0.44	4.56±0.27	11.31±0.80	14.02±0.62	9.84±0.58
GKVK 17 × ICGV 86590	8.38±0.69	7.34±0.26	10.06±0.73	19.71±0.63	7.01±0.29
<b>Shelling percentage</b>					
ICGV 13099 × ICGV 86590	64.25±2.45	55.15±4.29	61.97±1.50	58.52±0.86	52.12±0.59
GPBD 4 × ICGV 99005	57.53±4.68	59.04±2.46	49.96±4.65	55.82±0.88	50.66±0.63
<b>SMK (%)</b>					
ICGV 13099 × ICGV 86590	65.20±1.40	59.94±1.65	66.80±0.80	81.37±0.84	72.37±1.24
GPBD 4 × ICGV 99005	69.22±0.86	61.56±1.10	72.40±0.87	71.08±1.14	78.71±1.03

**Table 2a:** Mean and standard error of various generations for late leaf spot disease reaction in groundnut

Traits	P <sub>1</sub>	P <sub>2</sub>	F <sub>1</sub>	F <sub>2</sub>	F <sub>3</sub>
<b>PDI 65<sup>th</sup> DAS</b>					
GPBD 4 × TMV 2	14.62±0.20	17.07±0.52	19.71±0.50	3.38±0.28	2.43 ± 0.16
GKVK 17 × ICGV 86590	16.14±0.33	11.80±1.11	20.60±0.40	6.45±0.39	5.76±0.28
<b>PDI 75<sup>th</sup>DAS</b>					
GPBD 4 × TMV 2	30.43±0.17	31.97±0.53	22.54±1.19	7.24±0.56	6.16±0.31
GKVK 17 × ICGV 86590	35.28 ± 0.40	16.40 ± 2.18	45.20±0.37	12.30±0.74	13.20±0.68
<b>PDI 90<sup>th</sup>DAS</b>					
GPBD 4 × TMV 2	35.89 ± 0.24	43.31±0.33	27.67±1.33	12.46±0.94	11.93±0.55
GKVK 17 × ICGV 86590	36.18 ± 0.47	24.80±1.59	53.20±0.37	22.95±1.43	20.42±1.14
<b>PDI 115<sup>th</sup>DAS</b>					
GPBD 4 × TMV 2	44.08 ± 0.39	71.80±1.15	35.69±2.15	26.50±0.80	33.16±0.98
GKVK 17 × ICGV 86590	56.00±3.31	28.40±1.43	56.02±2.92	29.04±1.55	28.35±1.30

**Table 3:** Estimates of gene effects for growth, yield and yield attributing traits in four crosses of groundnut

Traits	Cross	m	$[\hat{d}]$	$[\hat{h}]$	$\chi^2$ Statistics	probability	Adequacy of additive - Dominance model
Days to first flowering	GPBD 4 × TMV 2	31.22**±0.17	-0.70±0.20	9.47**±0.65	122.34	0.00	Not adequate
	GKVK 17 × ICGV 86590	33.21**±0.12	1.62±0.26	-0.10±0.43	161.36	0.00	Not adequate
Plant height (cm)	GPBD 4 × TMV 2	26.80**±0.21	-7.57±0.27	-3.9±0.46	231.86	0.00	Not adequate
	GKVK 17 × ICGV 86590	28.01**±0.33	8.50*±0.35	-6.63*±0.52	464.27	0.00	Not adequate
Primary branches/plant	GPBD 4 × TMV 2	4.34*±0.09	0.14±0.15	1.86±0.25	306.23	0.00	Not adequate
	GKVK 17 × ICGV 86590	3.47*±0.03	0.41±0.03	7.31*±0.17	452.05	0.00	Not adequate
Pods /plant (g)	GPBD 4 × TMV 2	22.53*±0.94	1.47±1.05	3.19±1.01	125.98	0.00	Not adequate
	GKVK 17 × ICGV 86590	18.77*±0.30	-0.78±0.32	10.19**±0.51	351.49	0.00	Not adequate
Pod yield/plant (g)	GPBD 4 × TMV 2	10.35**±0.24	2.42±0.24	8.07*±0.31	139.09	0.00	Not adequate
	GKVK 17 × ICGV 86590	14.92**±0.42	0.39±0.48	2.37*±0.68	310.42	0.00	Not adequate
Kernel yield /plant (g)	GPBD 4 × TMV 2	6.69*±0.24	1.88±0.26	7.95*±0.75	52.72	0.00	Not adequate
	GKVK 17 × ICGV 86590	7.26*±0.28	0.07±0.32	6.17*±0.77	278.07	0.00	Not adequate
Shelling percentage	GPBD 4 × TMV 2	6.69*±0.24	1.88±0.26	7.95*±0.75	52.72	0.00	Not adequate
	GKVK 17 × ICGV 86590	7.26*±0.28	0.07±0.32	6.17*±0.77	278.07	0.00	Not adequate
SMK (%)	GPBD 4 × TMV 2	68.55**±1.13	1.57±1.33	0.68±1.44	19.97	0.00	Not adequate
	GKVK 17 × ICGV 86590	70.36**±0.47	9.42*±0.50	13.30*±1.42	741.70	0.00	Not adequate

**Table 3a:** Estimates of genetic parameters for growth, pod yield and yield attributing traits in groundnut

Traits	Cross	M	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	$[\hat{l}]$	Types of di-genic epistasis
Days to first flowering	GPBD 4 × TMV 2	38.24**±0.42	-0.30±0.02	8.23**±1.07	5.73*±1.28	-39.82**±17.69	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	35.21**±0.03	-0.25±0.55	1.62±0.94	1.22*±1.22	-19.30*±3.73	Duplicate epistasis between dominance increasing effect genes
Plant height (cm)	GPBD 4 × TMV 2	15.97**±0.44	-1.00±0.32	-	-	94.64**±3.85	Duplicate epistasis between dominance decreasing effect genes
	GKVK 17 × ICGV 86590	21.47**±0.42	7.68**±0.37	-	-	112.63**±5.57	Duplicate epistasis between dominance decreasing effect genes
Primary branches/plant	GPBD 4 × TMV 2	6.26**±0.12	-.20±0.15	1.56±0.34	0.16±0.48	-13.77**±1.25	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	7.19**±0.12	0.30±0.03	1.95*±0.36	1.67±0.41	-16.21*±1.38	Duplicate epistasis between dominance increasing effect genes
Pods /plant (g)	GPBD 4 × TMV 2	42.78**±1.75	2.0±2.2	47.77**±4.16	48.17**±5.13	-	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	48.73**±1.45	-0.51±0.33	70.61**±3.26	60.30**±3.78	-	Duplicate epistasis between dominance increasing effect genes
Pod yield/plant (g)	GPBD 4 × TMV 2	26.22**±1.19	2.78*±0.24	18.27**±3.30	15.42**±3.35	-68.66**±10.59	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	36.20**±1.17	-0.35±0.54	45.43**±2.75	42.78**±3.28	-172.09**±3.28	Duplicate epistasis between dominance increasing effect genes
Kernel yield /plant (g)	GPBD 4 × TMV 2	14.02**±0.62	1.66±0.26	9.34**±2.06	7.60**±4.19	-29.54**±6.27	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	19.71**±0.63	0.52±0.37	27.42**±1.56	26.26**±1.91	-93.44**±5.67	Duplicate epistasis between dominance increasing effect genes
Shelling percentage	GPBD 4 × TMV 2	43.75**±0.26	-	4.44*±4.55	-	72.93**±17.91	Complementary epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	72.02**±0.107	-	-0.38*±5.19	-	-82**±20.69	Complementary epistasis between dominance decreasing effect genes
SMK (%)	GPBD 4 × TMV 2	64.93**±1.53	3.0*±1.53	-19.43*±4.94	-	56.58**±14.60	Duplicate epistasis between dominance decreasing effect genes
	GKVK 17 × ICGV 86590	555.02**±0.73	5.50**±2.43	20.19*±3.69	24.78**±6.59	-27.67**±12.95	Duplicate epistasis between dominance increasing effect genes

**Table 4:** Test for inheritance pattern for resistance to LLS disease in F<sub>2</sub> population derived from four crosses in groundnut

Cross	Parent /generation	Observed number of F <sub>2</sub> plants					Observed ratio	Expected ratio	Expected number of F <sub>2</sub> plants				$\chi^2$ statistic	$\chi^2 > P @ 0.05$
		Total	R	MR	MS	S			R	MR	MS	S		
GPBD 4 × TMV 2	GPBD 4	5	5	0	0	0	-	-	5	0	0	0	-	-
	TMV 2	5	0	0	0	5	-	-	0	0	0	5	-	-
	F <sub>1</sub>	5	4	1	0	0	-	-	5	0	0	0	-	-
	F <sub>2</sub>	100	80	10	4	6	8:1:0.4:0.6	9:3:3:1	56.25	33.33	33.33	11.11	13.62	5.8
GKVK 17 × ICGV 86590	GKVK 17	5	0	0	5	0	-	-	0	0	5	0	-	-
	ICGV 86590	5	5	0	0	0	-	-	5	0	0	0	-	-
	F <sub>1</sub>	5	4	1	0	0	-	-	5	0	0	0	-	-
	F <sub>2</sub>	100	77	14	2	7	11:2:0.28:1	9:3:3:1	56.25	33.33	33.33	11.11	12.45	4.63

**Table 4a:** Test for inheritance pattern for resistance to LLS disease in F<sub>2</sub> population derived from four crosses in groundnut

Cross	Parent /generation	Observed number				Observed ratio	Expected ratio	Expected number		$\chi^2$ statistic	$\chi^2 < P @ 0.05$
		Total	R	MR	MS			R	S		
GPBD 4 × TMV 2	GPBD 4	5	5	0	0	-	-	0	0	-	-
	TMV 2	5	0	0	0	-	-	0	5	-	-
	F <sub>1</sub>	5	4	1	0	-	-	0	0	-	-
	F <sub>2</sub>	100	80	10	4	15.66:1	15:1	93.75	6.25	0.002	3.89
GKVK 17 × ICGV 86590	GKVK 17	5	0	0	5	-	-	0	0	-	-
	ICGV 86590	5	5	0	0	-	-	0	0	-	-
	F <sub>1</sub>	5	4	1	0	-	-	0	0	-	-
	F <sub>2</sub>	100	77	14	2	15.1	15.1	93.75	6.25	0.04	3.89

HR: Highly resistant; R: Resistant; MR: Moderately resistant; S: Susceptible

**Table 4b:** Number of families exhibiting reaction to LLS disease in F<sub>3</sub> population derived from four crosses in groundnut

Cross	R (families)	MR (families)	MS (families)	S (families)	Total (families)
GPBD 4 × TMV 2	70	16	7	5	98
GKVK 17 × ICGV 86590	71	17	5	3	96

HR: Highly resistant; R: Resistant; MR: Moderately resistant; S: Susceptible

**Table 5:** Estimates of gene effects for LLS disease reaction in four crosses of groundnut

Traits	Cross	m	$\hat{d}$	$\hat{h}$	$\chi^2$ Statistics	probability	Adequacy of additive - Dominance model
PDI @ 65 <sup>th</sup> DAS	GPBD 4 × TMV 2	6.27*±0.19	5.88*±0.23	0.05±0.552	2521.2	0.00	Not adequate
	GKVK 17 × ICGV 86590	4.06**±0.32	10.46**±0.4	13.47*±0.57	504.71	0.00	Not adequate
PDI @ 75 <sup>th</sup> DAS	GPBD 4 × TMV 2	25.27**±0.25	4.02±0.26	-	2271	0.00	Not adequate
	GKVK 17 × ICGV 86590	6.59*±0.65	27.42**±0.72	36.80*±0.80	630.64	0.00	Not adequate
PDI @ 90 <sup>th</sup> DAS	GPBD 4 × TMV 2	37.75**±0.20	-3.15±0.20	-	1436.58	0.00	Not adequate
	GKVK 17 × ICGV 86590	23.79**±0.70	11.29*±0.74	28.60*±0.82	264.72	0.00	Not adequate
PDI @ 115 <sup>th</sup> DAS	GPBD 4 × TMV 2	53.93**±0.56	-	-	327.73	0.00	Not adequate
	GKVK 17 × ICGV 86590	31.15**±1.33	6.23*±1.60	7.95*±3.13	99.69	0.00	Not adequate

C<sub>1</sub>= ICGV 13099 × ICGV 86590, C<sub>2</sub>= GPBD 4 × ICGV 99005 C<sub>3</sub>= GPBD 4 × TMV 2 C<sub>4</sub>=GKVK 17 × ICGV 86590**Table 6:** Estimates of genetic parameters for late leaf spot disease reaction in groundnut

Traits	Cross	m	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{l}$	Types of di-genic epistasis
PDI @ 65 <sup>th</sup> DAS	GPBD 4 × TMV 2	3.38**±0.28	-1.22±0.28	13.41**±0.79	7.10**±0.91	38.46**±2.75	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	6.45**±0.39	2.17*±0.58	11.28**±1.12	8.99**±1.32	33.99**±3.66	Duplicate epistasis between dominance increasing effect genes
PDI @ 75 <sup>th</sup> DAS	GPBD 4 × TMV 2	7.24**±0.56	-0.76±0.28	13.09**±1.60	20.21**±1.77	34.99**±5.74	Duplicate epistasis between dominance decreasing effect genes
	GKVK 17 × ICGV 86590	12.32**±0.74	9.44**±1.10	19.54**±2.36	19.42**±2.53	92.42**±7.04	Duplicate epistasis between dominance decreasing effect genes
PDI @ 90 <sup>th</sup> DAS	GPBD 4 × TMV 2	12.46**±0.94	-3.71**±0.20	11.54**±2.55	16.05**±2.74	37.72**±8.85	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	22.95**±1.43	5.69**±0.83	26.91**±4.20	15.58**±4.25	67.15**±13.06	Duplicate epistasis between dominance increasing effect genes
PDI @ 115 <sup>th</sup> DAS	GPBD 4 × TMV 2	26.50**±0.80	-	-	-	60.05**±10.11	Duplicate epistasis between dominance increasing effect genes
	GKVK 17 × ICGV 86590	29.04**±1.55	13.85**±0.61	11.65**±3.40	17.10**±3.23	68.22**±16.22	Duplicate epistasis between dominance increasing effect genes

C<sub>1</sub>= ICGV 13099 × ICGV 86590 C<sub>2</sub>= GPBD 4 × ICGV 99005 C<sub>3</sub>= GPBD 4 × TMV 2 C<sub>4</sub>=GKVK 17 × ICGV 86590

## Conclusion

Inferences based on the magnitude 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 might have influenced 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 suggesting appropriate breeding method that should be followed to achieve higher expression of such characters.

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