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Inter-allelic interactions in the inheritance of physical-quality traits in peanut (*Arachis hypogaea* L.)

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Abstract

Genetic models presume the absence of inter-allelic interactions (epistasis), while estimating components of genetic variation, may lead to biased estimates. Genetic control of physical quality traits in peanut and role of epistasis was studied following a triple test cross mating design. The experimental materials consisting of 27 progenies produced by crossing nine inbred lines belonging to both Spanish and Virginia botanical groups with three testers (TAG 24, TMV 2 NLM, and their F_1) were evaluated in a replicated randomized complete block design. The data on parents, F_1s and three-way crosses were collected for 10 physical-quality traits of pods and kernels following standard procedures, and analysed to detect epistasis. Inter-allelic interactions were detected for shelling outturn, 100-pod weight, count, 100-seed weight, sound mature seeds, pod length, seed diameter and ratio of seed length to seed diameter using *F* or *t* statistics. For pod diameter and seed length, epistasis could not be detected by both the tests, and in the expression of these two traits additive gene action was very important. Partitioning of total epistasis to its component parts indicated presence of both additive × additive (*i*) type and additive × dominance (*j*) + dominance × dominance (*l*) type inter-allelic interactions for 100-seed weight with the preponderance of the former indicating that it can be effectively exploited. Inheritance of 100-pod weight was controlled by *i* type of inter-allelic interactions, shelling outturn was controlled by *j+l* type. The findings suggest that improvement in physical-quality traits, especially pod and seed size can be achieved through conventional breeding, but it would be necessary to delay the selection process until maximum frequency of homozygous loci is achieved to exploit *i* type epistasis.

Keywords. *Arachis hypogaea*; Epistasis; Inheritance; Peanut; Quality traits; Triple test cross.
Abbreviations: ANOVA_analysis of variance, HPW_100-pod weight, HSW_100-seed weight, PD_pod diameter, PL_pod length, SD_seed diameter, SL_seed length, SMS_sound mature seeds, SOT_shelling outturn, TTC_triple test cross

Introduction

Peanut (*Arachis hypogaea* L.), an annual legume grown in more than 100 countries, is widely used as an edible oilseed crop because of its high oil content (36-54% on dry matter basis) and as a direct source of human food as it contains easily digestible protein (12-36%) in its seeds. About 38.38 million metric tonnes of peanuts in shell are produced globally from 23.52 million hectares with an average yield of 1634 kg ha^{-1} (FAO Stat., 2011). In India, it is primarily a source of high quality edible oil, while in many countries including India it also finds its use as food and confectionery item because of its high energy value, high protein content, low cholesterol nature, and presence of some of the essential vitamins and minerals. During past three decades use of peanut for food and confectionery purposes is on the rise whilst its utilization for oil extraction is on the decline mainly because of availability of other cheaper vegetable oils (Hariprasanna et al., 2008). This trend is not only adding to crop diversification of peanut, but also inspiring peanut researchers to popularize peanuts as a food crop for ensuring nutritional security for otherwise nutritionally deprived populations particularly in the underdeveloped world. The genetic gain for peanut yield in India came from improvement in seed size, seed weight, and number of pods per plant (Rathnakumar et al., 2012). Thus, breeding for large-seeded peanuts suited for confectionery purposes has gained momentum over the years. Various physical, sensory, chemical and nutritional factors determine the quality of peanut seed (Dwivedi and Nigam, 2005). Shape and size of pods as well as seeds are important determinant of market price, particularly when the peanuts are used as food. Consequently, development of genotypes having high yielding potential coupled with appropriate pod and kernel physical characteristics, the attributes that always fetch premium price in the market, is the important objective in peanut breeding.

Information on genetic control of quantitative traits is essential for planning a suitable breeding strategy aimed at simultaneous improvement in the attributes finally contributing to enhanced yield, and in the present case the value addition in farm produce to enable the peanut farmers to earn more per unit area of peanut they grow. In peanut, many researchers have worked out the genetic control of pod yield and related components. Some of the earliest studies have reported significant additive gene effects (Garet, 1976; Singh and Labana, 1980) or GCA variances (Wynne et al., 1975; Nava and Layrisse, 1987) for most of the economic traits in peanut. Significant reciprocal effects in the expression of pod yield and other economically important traits have also been reported (Garet, 1976; Gan et al., 1981; Dwivedi et al., 1989; Vindhiyavarman, 2000; 2001), indicating the role of maternal parent in the expression, and thus importance of selecting the parents while making crosses.

Reports on the nature of gene action involved in the expression of physical-quality traits are scanty. Seed size,

expressed in terms of 100-seed weight, is reported to be predominantly under the control of additive gene action or GCA variance (Labana et al., 1981; Dwivedi et al., 1989; Anderson et al., 1993). However, some of the reports have suggested importance of both additive and non-additive gene action in controlling seed size (Parmar et al., 2000). For other quality related traits like proportion of sound mature seeds and shelling outturn also both additive and non-additive gene effects have been reported to be important (Dwivedi et al., 1989). But some other studies have suggested predominant role of SCA estimates or non-additive gene effects (Wynne et al., 1975; Garet, 1976; Vindhiyavarman, 2000; 2001) in the control of these traits. A more recent study has reported that expression of majority of the physical-quality traits is regulated predominantly by additive gene action suggesting possibility of early generation selection, while non-additive gene action also plays an equally important role in the control of these traits, especially seed size (Hariprasanna et al., 2008). Existence of significant reciprocal effects for all the traits (Hariprasanna et al., 2008) denoted role of maternal parent in the regulation of quality traits, thus highlighting importance of selection as well as appropriate use of parents in breeding for quality improvement.

Most of the studies on inheritance of quantitative traits of peanut have used genetic models, which assume absence of inter-allelic interactions. Information on the role of inter-allelic interactions (epistasis) particularly in the expression of the physical-quality traits is scanty. Because of self-pollination in peanut, variation due to dominance effects and their interactions cannot be effectively exploited. However, additive × additive (*i* type) epistatic variation is useful as it can be fixed in homozygous cultivars. This study, therefore, was taken up to determine the importance of epistasis in the expression of physical-quality traits of pods and kernels in peanut, and to obtain estimates of additive and dominance variances for these traits, if not influenced by epistasis.

Results and discussion

Quantitative genetic variations

The ANOVA revealed significant genotypic differences among the plant material for all the 10 traits studied (Table 1). Except for seed diameter, inbred lines used in the present study were diverse for all the physical-quality traits studied as indicated by the significant contribution of parents to the variation for these traits. This was further supported by the significant differences observed among the crosses for all the traits. Though considerable variations were observed among the nine lines for physical quality traits related to seed-yield (SOT, HSW, count and SMS) (Fig. 1) and seed-shape (SL and SL/SD) (Fig.2), the range of variations were of different magnitudes as indicated by the standard deviation (SD) of means observed for a trait across the lines. The testers differed significantly only for five traits *viz*., shelling outturn, 100-seed weight, sound mature seeds, seed length and ratio of seed length to seed diameter. Except for shelling outturn and ratio of seed length to seed diameter, the significant contribution of crosses observed for different traits was independent of a line or a tester involved in a cross as evident from the non-significant line × tester effects observed for these traits (Table 1).

Detection of epistasis

Many genes that act singly and in interaction with each other affect quantitative traits. Epistasis, the interaction between genes at different loci, may exert important effects on (a) the dynamics of evolving populations (Cheverud and Routman, 1996), (b) changes of genetic variances caused by long-term selection (Carlborg et al., 2006) or by a population bottleneck (Goodnight, 1987), and (c) heterosis (Kusterer et al., 2007; Melchinger et al., 2007). In general, the mating designs usually adopted in the breeding programmes assume absence of epistasis. But in the presence of epistasis the estimates of genetic components obtained would be biased, thus affecting the choice of suitable breeding strategy.

The ANOVA for detection of epistasis revealed significant overall epistasis ($L_{1}j + L_{2}j - 2L_{3}j$) in the expression of shelling outturn, 100-seed weight, sound mature seeds and seed diameter (Table 2). Both additive (*i)* and non-additive (*j+l*) interactions were significant for 100-seed weight, where *i* type of epistasis was greater in magnitude compared to *j+l* type epistasis detected for this trait. Only *i* type epistasis was detected for 100-pod weight and seed diameter, whereas for shelling outturn only *j+l* type of epistasis was observed. For traits, namely count, sound mature seeds, pod length, pod diameter, seed length and ratio of seed length to seed diameter, *F* test could not detect any epistasis. Mean squares due to sums ($L_{1j} + L_{2j}$) were significant for shelling outturn, 100-pods weight, count, 100-seed weight, sound mature seeds and seed length, whereas mean squares due to differences ($L_{1j} - L_{2j}$) were not significant for any of the trait studied. Correlation coefficients between sums and differences, which indicate the direction of dominance and type of genes exhibiting dominance, were non-significant for all the traits suggesting that dominant genes had both positive and negative effects for these traits (Table 2).

Though only three of the total nine lines used to detect epistasis belonged to Virginia type, out of 30 instances of this group significant epistatic deviations were detected in five by *t*-test compared to two significant epistatic deviations observed in Spanish type out of 60 instances, accounting for 16.7% and 3.3% of the total instances of their respective botanical groups, respectively. In Spanish group, the lines Chico and GG 2, contributed significantly to one instance each whereas, in Virginia group, NRCG 1022 and ICGV 98383, each contributed to three significant instances (Table 3). As reported earlier in peanut (Upadhyaya and Nigam, 1998; 1999, Aruna and Nigam, 2009), the manifestation of epistasis is genotype dependent. This reinforces the need to include several genotypes in studies designed to detect epistasis (Upadhyaya and Nigam, 1998; 1999). Also, it has been reported that epistatic effect was induced by stress level and mode of inheritance of some quantitative traits varied with the biotic or abiotic stress level (Fethi et al., 2011), thus necessitating use of several genotypes with varied response to different biotic and abiotic stresses. Further, both *F* and *t*-tests should be employed to detect the presence of epistasis because in some cases an *F*-test may fail to detect epistasis. Such a situation occurred in case of count, pod length and ratio of seed length to seed diameter, where *F*-test failed to detect presence of epistasis (Table 2). However, when *t*-test was used, lines were found to contribute to epistatic interactions in the expression of these traits (Table 3). These inconsistencies in detecting epistasis may arise because *F*-test detects whether lines differ in their contributions to expression of epistasis while, the *t*-test detects whether epistatic deviations of lines are significantly different from zero (Upadhyaya and Nigam, 1999). In the situations where the epistatic deviations are of equal magnitude and same sign, the *F*-test may fail to detect epistasis for a given trait.

The procedure used in this study provides for a test for epistasis that is valid regardless of gene frequencies, degree

Table 1. Analysis of variance for different physical-quality traits in peanut.

Source of variation	Mean sum of squares										
	df	SOT (%)	HPW (g)	Count	HSW (g)	SMS (%)	PL (cm)	PD (cm)	SL (cm)	SD (cm)	SL/SD
Replicates	2	28	1470 ***	2682 ***	240 ***	147	0.05	0.01	0.02	0.01	28.5
Treatments	38	299 ***	413 ***	1051 ***	99 ***	1092***	0.19 ***	0.04 ***	0.05 ***	0.01 **	299.4 ***
Parents	11	365 ***	390 **	1633 ***	152 ***	1216 ***	0.24 ***	0.09 **	0.07 ***	0.00	365.2 ***
Parents (Line)	8	456 ***	347 *	1933 ***	164 ***	1373 ***	0.26 ***	0.04 **	0.07 ***	0.00	455.8 ***
Parents (Testers)	2	153 **	30	364	108 *	936*	0.04	0.01	0.04 *	0.01	152.8 **
Parents (L *vs.* T)	1	66	1459**	1776 *	145 *	524	0.49 **	0.01	0.11 **	0.00	65.6
Parent *vs.* Crosses	1	66	146	147	157 *	1657**	0.25	0.02	0.02	0.02 *	66.2
Crosses	26	281 ***	434 ***	839 ***	75 ***	1018***	0.17 **	0.04 ***	0.05 ***	0.01 ***	280.5 ***
Line effect	8	699 ***	1225***	1885 **	165 **	1975 **	0.29	0.08 **	0.11 **	0.01	699.0 ***
Tester effect	2	169	52	89	70	2502 **	0.10	0.04	0.01	0.05 **	168.5
Line × Tester effect	16	85 ***	87	410	30	354	0.11	0.02	0.02	0.01	85.2 ***
Error	76	24	147	293	23	205	0.07	0.01	0.01	0.01	23.8
Total	116	114	257	582	52	495	0.11	0.09	0.03	0.06	114.2
Replicates	2	29	1501***	2055 **	202 **	122	0.05	0.00	0.01	0.01	0.019
Crosses	26	281 ***	434 **	839 **	75 **	1018 ***	0.17 *	0.04 ***	0.05 ***	0.01 **	0.099 ***
Line effect	8	699 ***	1224 ***	1885 **	165 **	1975 **	0.29	0.09 **	0.11 **	0.01	0.119 *
Tester effect	2	169	52	89	70	2502 **	0.10	0.04	0.01	0.05 **	0.525 ***
Line × Tester effect	16	85 **	87	410	30	354	0.11	0.02	0.02	0.01	0.036
Error	52	32	186	346	28	255	0.09	0.01	0.01	0.01	0.031
Total	80	113	299	549	47	499	0.11	0.02	0.02	0.01	0.053

SOT_shelling outturn; HPW_100-pod weight; HSW_100-seed weight; SMS_sound mature seeds; PL_pod length; PD_pod diameter; SL_seed length; SD_seed diameter.
*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

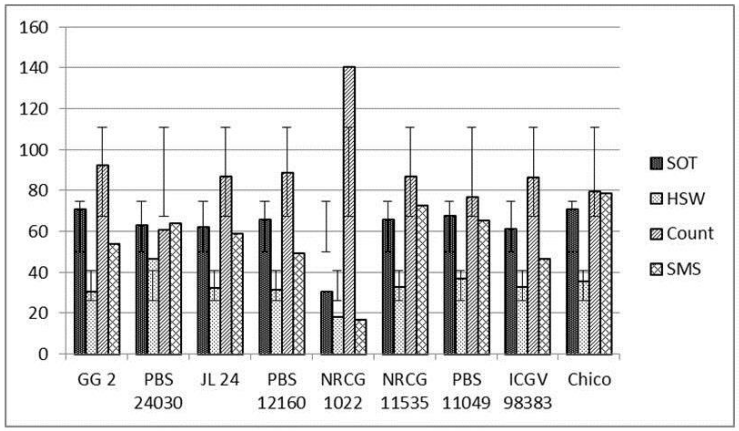

Fig.1. Means and standard deviations of nine lines for quality-seed traits related to seed-yield.
SOT_shelling outturn; HSW_100-seed weight; SMS_sound mature seeds

Table 2. Mean squares for epistatic, additive and dominance components for different physical-quality traits in peanut.

Source of variation	df	SOT (%)	HPW (g)	Count	HSW (g)	SMS (%)	PL (cm)	PD (cm)	SL (cm)	SD (cm)	SL/SD
Epistatic component											
Total epistasis	9	294*	467	2131	246**	3087*	0.44	0.04	0.05	0.05*	0.30
Error	18	89	808	1268	64	1208	0.22	0.05	0.05	0.02	0.15
i type epistasis	1	5	606*	520	643*	16261	0.96	0.21	0.04	0.16*	2.03
Error	2	115	15	778	29	970	0.28	0.07	0.04	0.01	0.12
J + *l* type epistasis	8	330*	449	2332	196*	1440	0.37	0.02	0.06	0.03	0.08
Error	16	86	907	1329	68	1238	0.21	0.05	0.05	0.02	0.16
Additive component											
Sums (L_{1j} + L_{2j})	8	694*	1430**	2123*	203*	2287*	0.36	0.10	0.12*	0.01	0.17
Error	16	71	304	704	58	660	0.17	0.04	0.03	0.01	0.07
Dominance component											
Difference (L_{1j} – L_{2j})	8	231	196	862	56	938	0.33	0.06	0.06	0.01	0.01
Error	16	111	173	729	46	524	0.32	0.03	0.04	0.02	0.07
Correlation		0.14	0.07	–0.007	–0.05	–0.15	–0.28	0.24	–0.27	–0.18	–0.04

SOT_shelling outturn; HPW_100-pod weight; HSW_100-seed weight; SMS_sound mature seeds; PL_pod length; PD_pod diameter; SL_seed length; SD_seed diameter.
*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

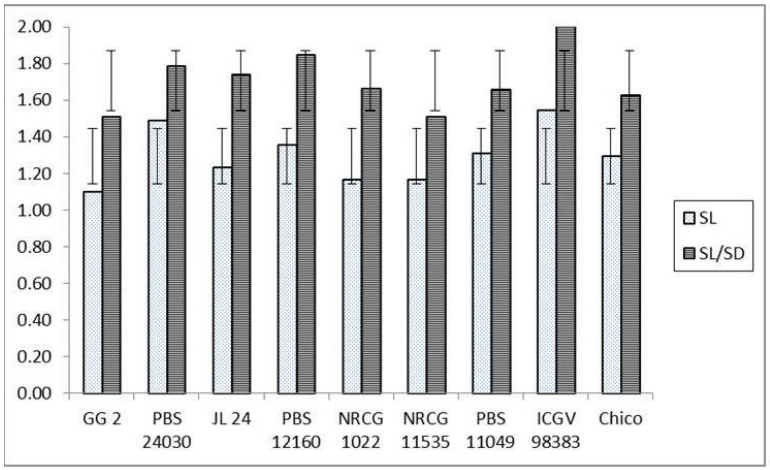

Fig.2. Means and standard deviations of nine lines for quality-seed traits related to seed-shape.
SL seed length; SL/SD ratio of seed length to seed diameter

Table 3. Epistatic deviations as detected by *t* test for traits exhibiting significant differences among lines.

Lines	SOT (%)	HPW (g)	Count	HSW (g)	SMS (%)	PL (cm)	PD (cm)	SL (cm)	SD (cm)	SL/SD
Chico	57.0	75.6	75.0	29.9	44.7*	2.5	1.1	1.3	0.7	1.7
GG 2	67.6	75.1	94.8	31.3	50.0	2.5	1.1	1.3	0.8	1.7*
JL 24	62.4	91.6	88.2	32.4	58.8	2.6	1.1	1.2	0.7	1.7
PBS 12160	65.2	71.7	98.6	29.9	43.5	2.6	1.2	1.3	0.7	1.9
NRCG 11535	62.2	86.0	93.0	31.0	63.0	2.4	1.2	1.2	0.7	1.6
PBS 11049	67.2	91.1	78.7	37.2	63.9	2.8	1.2	1.4	0.7	1.8
PBS 24030	63.2	106.5	69.7	40.2	56.9	3.0	1.4	1.5	0.8	1.9
NRCG 1022	39.6*	79.7	121.4	25.9	17.2	2.7*	1.3	1.2	0.7	1.8*
ICGV 98383	57.6	85.8*	97.1*	31.1*	38.0	2.8	1.3	1.4	0.7	1.9

SOT_shelling outturn; HPW_100-pod weight; HSW_100-seed weight; SMS_sound mature seeds; PL_pod length; PD_pod diameter; SL_seed length; SD_seed diameter.
*P ≤ 0.05.

Table 4. Estimates of additive (D) and dominance (H_1) components of variance for traits not showing significant epistasis.

Traits	D	H_1	$(H_1/D)^{½}$
PD (cm)	0.08	0.04	0.70
SL (cm)	0.12*	0.02	0.41

PD_pod diameter; SL_seed length; *P ≤ 0.05.

of inbreeding and linkage relationships (Ketata et al., 1976). Because epistasis was detected for majority of the traits studied, either by *F*-test or *t*-test, the estimates of additive (*D*) and dominance (*H*) components of variance for these traits would have been biased had they been estimated by the procedures assuming absence of epistasis. The *i* type of epistasis observed for 100-pod weight and seed diameter, which is fixable in the homozygous state, can be exploited in a breeding programme through simple pedigree selection. In case of 100-seed weight also proportion of epistasis which is due to *i* type of inter-allelic interactions has been observed to be greater in magnitude as compared to the corresponding (*j+l*) type of inter-allelic interactions though both are significant, the former is fixable and can be exploited in the genetic enhancement of this trait. In cases where *i* type of epistasis has been detected, selections in early generations will not be effective. To exploit *i* type of inter-allelic interactions observed for 100-pod weight, 100-seed weight and seed diameter, large populations should be carried forward for selection for these traits in later generations, when maximum homozygosity of favourable gene combinations is attained. This shall be an important approach to develop peanut genotypes with desired pod and seed size.

For the improvement of pod diameter and seed length, for which epistatic interactions were found to be absent and additive gene action was more important compared to the dominant gene action (Table 4), selection in the early generations itself will be effective. Degree of dominance $[(H_1/D)^{½}]$ was in the range of partial or incomplete dominance for these traits.

Choice of testers for detection of epistasis is very important as measured epistasis refers only to the loci for which the testers differ. Discrepancies may arise from the genetic differences among the testers used. The testers (TAG 24 and TMV 2 NLM) used in this study, belonged to different botanical groups. Though this single pair of testers used in this study has been able to detect epistasis for majority of the traits studied, use of two or more pairs of testers could have lead to better resolution. Alternatively, use of more locations would have helped in improving detection of epistasis. However, the difficulty in obtaining sufficient hybrid seeds in peanut restricts the use of more tester pairs or evaluation at multiple locations.

Materials and Methods

Plant material and experimental design

The experimental material evaluated in this study was developed by following a triple test cross (TTC) mating design (Kearsey and Jinks, 1968) at the Directorate of Groundnut Research, Junagadh, India. Two peanut genotypes, *viz.*, TAG 24 and TMV 2 NLM (hereafter referred to as L_1 and L_2, respectively) were used as testers and crossed in the rainy season of 2008 and 2009 to produce the third tester, the F_1 hybrid (designated as L_3). TAG 24 is a semi-dwarf and early maturing commercial Spanish variety having small pods and kernels, high yield and very high harvest index (Patil et al., 1995). TMV 2 NLM, a late maturing Virginia germplasm line having medium bold pods and kernels, is an induced narrow leaf mutant of an Indian peanut variety, TMV 2. The three testers (L_1, L_2 and L_3) were crossed in the rainy season of 2009 with nine true breeding lines from diverse sources. These lines, varied widely for pod and kernel dimensions with small pods and kernels (Chico) to bold pods and kernels (PBS 24030). The lines consisted of six Spanish (*Arachis hypogaea* ssp. *fastigiata* var. *vulgaris*) (Chico, GG 2, JL 24, PBS 12160, NRCG 11535, PBS 11049) type and three Virginia (*Arachis hypogaea* ssp. *hypogaea* var. *hypogaea*) (ICGV 98383, PBS 24030, NRCG 1022) type peanut genotypes; four of them (GG 2, JL 24, PBS 12160 released as Girnar 3, and PBS 24030 released as Girnar 2) were improved varieties released for different agro-climatic situations in India.

The testers were used as males in the entire TTC combinations. The experimental material consisted of 11 inbred lines (L_1, L_2 and 9 inbred lines), 19 single crosses (18 single crosses and L_3 tester), and nine three-way crosses altogether leading to 39 populations (Supplementary Table 1). These 39 populations were raised in a randomized complete block design with three replicates at the Experimental Farm of the Directorate of Groundnut Research, Junagadh (70.36°E longitude and 21.31°N latitude, 60 m above MSL) in summer 2010 (Supplementary Table 2). Each population was grown in five rows of 3 m length per replication (plot size of 9 m^2) with a row-to-row distance of 60 cm and plant-to-plant distance of 10 cm. The experimental material was bordered by a standard groundnut variety to avoid border effect. The soil type was medium black and calcareous. The agronomic package of practices recommended for the region was followed to raise the crop.

Observations on physical-quality traits

Ten plants were randomly selected replication-wise in each genotype and harvested individually at maturity. Observations were recorded after drying the produce to uniform moisture content of below 10%. The shelling outturn was calculated as per cent recovery of seeds on shelling of pods from bulked samples replication-wise. Weight of randomly selected 100-pods (g) and 100-seeds (g) was recorded replication-wise. The number of seeds in one ounce (28.4 g) was calculated to obtain the count. To measure the proportion of sound mature seeds the number of fully matured seeds out of randomly sampled seeds was counted and expressed in percentage. Average of 25 randomly selected pods in each replication was taken to record pod length (cm) and pod diameter (cm). Pod length was recorded by arranging pods from end-to-end along the length of the pods, and for pod diameter pods were arranged along the width of the pods. Similarly, 25 randomly selected seeds were used to record seed length (cm) and seed diameter (cm). Ratio of seed length to seed diameter (SL/SD) which expresses the seed-shape was recorded by dividing seed length with seed diameter.

Statistical analysis

The method used to detect epistasis was based on triple test cross outlined by Kearsey and Jinks (1968) and as modified by Ketata et al. (1976). The genetic model used is;

$L_{ijk} = \mu + g_{ij} + r_k + e_{ijk}$

where,

L_{ijk} = Phenotypic value of cross between tester *i* and line *j* in *k* replication

μ = Overall mean of all single and three way crosses

g_{ij} = Genotypic value of cross between tester *i* and line *j*

r_k = Effect of k^{th} replication

e_{ijk} = Error

In the analysis of variance (ANOVA), the presence of epistasis was indicated, if the mean squares for deviations ($L_{1j} + L_{2j} - 2L_{3j}$ where, *j* is j^{th} line crossed to L_1, L_2 and L_3 testers in L_{1j}, L_{2j} and L_{3j} crosses, respectively) were significantly greater than pooled error, as evaluated by an *F*-test. However, when all the deviations are of the same sign

and of comparable magnitude, the *F*-test in ANOVA would fail to detect the epistasis even though it may be present. To cope with this situation, a *t*-test was used on mean deviations to detect the significance of epistasis (Upadhyaya and Nigam, 1999). Further, the sum of squares due to epistasis was partitioned into sum of squares due to *i* (additive × additive) type of epistasis and due to *j* + *l* (additive × dominance + dominance × dominance) type of epistasis (Jinks and Perkins, 1970) and their significance was tested against their respective interactions with blocks. In case of absence of epistasis for a trait, additive (*D*) and dominance (H_1) components of variation were estimated from mean squares due to sums and differences, respectively. The direction of dominance was determined by the correlation coefficient between corresponding sums ($L_{1j} + L_{2j}$) and the differences ($L_{1j} - L_{2j}$) of lines. Average degree of dominance was calculated as $(H_1/D)^{1/2}$.

Conclusions

The present study has detected role of epistasis in the inheritance of some of the physical-quality traits in peanut. The results have implications on breeding and selection procedures for tailoring peanut genotypes with desired physical-quality traits of pods and kernels. For improving seed length, for which epistasis was absent and additive gene action was more pronounced in the inheritance, selection in the early generations will be effective. For traits where *i* type of gene action has been detected (HPW, HSW and SD), the selection procedures have to be amended in a way to utilize the additive × additive type of gene interactions. This includes maintenance of large populations prior to selection to give maximum chance for reconciliation of genes in advantageous combinations, followed by selection in later generations. Selection based on early generation testing would be ineffective in such cases. The maintenance of larger populations could particularly be required when exotic germplasm is used in the breeding programme as number of segregating loci is expected to be more in adapted × exotic crosses.

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