

Estimating genetic variability, gene effect, heritability, and genetic advance of yield component agronomic traits: towards the improvement of peanut agronomic traits

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Abstract

Background: Peanut is an important oil and legume food crop for human and feed for livestock. Peanut yield association characters like pod and seed traits are the most widely targeted parameter. Peanut yield is a function of growth rate, duration of reproductive growth, and the fraction of crop growth rate which are partitioned toward pod yield. For effective selection, heritability along with genetic advance is more useful than the estimation of only heritability.

Methods: The present study field design was laid out using single row and single plot techniques. Pod length, pod width, pod length by width, seed length, seed width, seed length by width yield contributing data were collected both from two parents and 251 RIL populations across two locations in two consecutive cropping seasons (2015/2016 & 2016/2017). Data analysis was computed through SAS ver.9.4 and PBTools ver.1.4.

Results: The highest genotypic coefficient of variation was found in pod length (22.47), number of pods per plant (23.66), pod yield per plant (28.43), multiple seedpods per plant (30.44). The highest narrow sense heritability was found in seed length (66%), pod length by width (87%), and pod thickness (93%), meanwhile, the highest broad sense heritability values have been recorded in seed length (99%), seed length by width (99%), number of pods per plant (95%), shelling percentage (94%), pod thickness (93%), thickness of pod shells (92), seed yield per plant (89%), seed thickness (87%), seed width (83%), multiple seedpods per plant (79%), and pod weight per plant (75%). The highest genetic advance as percent of mean values occurred in multiple seedpods per plant (215.44), number of pods per plant

(85.28), pod yield per plant (64.90), seed yield per plant (63.49), thickness of pod shells (56.87), pod length by width (36.55), seed length by width (30.98), and seed length (23.26).

Conclusions: Additive gene effects were observed in the traits of seed length, seed length by width, pod length, pod width, pod length by width, pod thickness, thickness of pod shells, and multiple seedpods per plant. The highest broad sense heritability values coupled with high genetic gain were estimated in multiple seedpods per plant, number of pods per plant, pod weight plant, seed weight per plant, thickness of pod shells, pod length by width, seed length by width. Therefore, in the present study, use more pod and seed-related traits than the previous findings.

Key words: Peanut; Heritability; Genetic advance, Additive gene effect; Dominant gene effect, PBTools;

Introduction

Peanut (*Arachis hypogaea* L.) is one of the kings of oilseeds with a multi-purpose legume crop grown and highly consumed in arid and semi-arid regions of the world. It is an economically important and versatile crop for resource-poor farmers in Asia and Africa that offers a rich source of oil, protein, minerals (Ca, Mg, P and K), and vitamins (E, K and B1) (Prabhu, Divyadharsini, and Manivannan 2015). Yield and yield contributing parameters are the most widely targeted traits of peanut improvement program across the globe. Peanut pod yield is a function of crop growth rate, duration of reproductive growth, and the fraction of crop growth rate partitioned toward pod yields. Therefore, understanding of physiology of yield is also essential for better target yield increase in crop including peanut. The main important yield contributing attributed traits are pod yield per plant, number of pods per plant, and 100-seed weight (Janila et al. 2013).

In peanut genetic variability is very low due to the origin of a single hybridization event between two different diploid species followed by a chromosome doubling and crossing barriers with wild diploid species due to the variation of ploidy nature. The cultivated groundnut is an allotetraploid, while all wild *Arachis* species are diploid except *A. monticola* and certain species in Section *Rhizomatosae*. The low genetic variability for the traits of interest and polyploidy nature are a major bottleneck for peanut improvement breeding strategies. The cultivated accession of *Arachis hypogaea* in the gene banks and the advanced breeding lines are frequently used as sources of variability used as parents in hybridization (Janila et al. 2013).

Segregating populations derived from crossing two parents are most common in peanut breeding programs. In peanut improvement program, segregating populations derived from hybridization through

pedigree and bulk-pedigree methods of breeding are the most common. Pedigree selection method allows breeders to practice selection of the best traits with high heritability values such as plant type, pod and seed-related traits and the testa color in early filial generations. Selection of quantitative traits such as yield and seed composition characters made in later generations. Bulk-pedigree method is a modified method of bulk aimed at improving traits with low heritability traits (Wynne and Gregory, 1981). Single seed decent method is becoming popular and it has the advantage to save space and resources (Isleib et al. 1994). G×E has a considerable influence on the progress of crop improvement. In peanut, a majority of important agronomic traits is polygenic nature and highly influenced by environment that hinders the achievable genetic gains in breeding programs. Genetic analysis of yield has revealed by the highly influence of the environment on pod yield traits (Zhang et al. 2011). High yielding cultivars with the least g×e interactions are normally desirable. However, when a cultivar is to be selected for a specific environment the g×e interaction is desirable for maximizing production (Janila et al. 2013).

Heritability is an idea of how much of the variation is available in a trait due to genetic factors. High heritability indicates a strong similarity between parents and their respective offspring with regard to a specific trait, while low heritability implies that low level of resemblance between them. The combined effect of all loci, including possible allelic interactions within each locus (dominance) and between loci (epistasis) is the effect of genotypic value. The effect of a particular allele on a trait is depends on the allele's frequency in the population and the effect of each genotype that includes all the allele. This is sometimes called as the average effect of an allele. The additive genetic value of an individual population called the breeding value is the sum of the average effects of all the alleles (Falconer & Mackay, 1996). According to the principles of Mendelian law of segregation one allele from each locus is present in each gamete cell, and in this way, additive genetic information are transferred from parents to offspring. Certainly in the reason of each offspring receives a different set of alleles from its parents, half of the additive genetic variance in the population occurs within families.

Narrow sense heritability is the proportion of phenotypic variance among individual population that is due to heritable genetic effects (additive). Broad sense heritability can estimated as the proportion of phenotypic variances directly attributable to the effect of the whole genotype, it comprising the sum total of additive, dominance and epistatic variance components (Nyquist 1991; Falconer and Mackay 1996). Heritability is a key parameter for quantitative genetics because it determines the response to selection. In the field of plant, breeding there are many different selection principles, and mating designs and the possibility of observational units are quite diverse, which are ranging from individual plant population to a

means of genotypes tested across multiple environments. Normally, no difference is made between broad- and narrow-sense heritability; however, narrow-sense (h^2) heritability is most important in animal and plant selection programs, because response to artificial natural selection depends on additive genetic variance. Moreover, resemblance between relatives is mostly driven by additive genetic variance (Hill et al. 2008). The values of heritability should be lies between 0 and 1. For example, narrow-sense heritability for humans' height is estimated 0.8 (Macgregor et al. 2006; Visscher et al. 2008).

Naturally, variation is classified into three main types such as phenotypic, genotypic, and environmental. Mather and Jinks (1982) stated that phenotypic variation is dividing into three main features viz; (1) heritable fixable (additive variance), (2) heritable non-fixable (dominance and epistasis variance) and (3) non-heritable non-fixable (environmental variance). Actually, the heritable fixable component of phenotypic variance will be included in additive x additive fraction of the epistasis variances. The genetic variances are consists of additive, dominance and epistasis components. In advance, the total phenotypic variations might be divided into (1) fixable (additive and additive x additive), (2) non-fixable (dominance, additive x dominance, dominance x dominance types of epistasis, and environmental fraction) components (Singh and Narayana 1990, 1993; Singh and Chaudary, 1999). Cockerham (1961) also reported the epistatic variation categorized as additive x additive, additive x dominance and dominance x dominance variances components. Many previous studies showed that epistatic gene action or non-allelic interaction effects in the inheritance of quantitative traits are very important for plant breeders' to select promising and outstanding plant population (Khattak et al. 2002; Sharma et al. 2003; Rebetzke et al. 2004; Sood et al. 2004).

Genetic variation is very important to maintain the level of high productivity crops including peanut breeding programs (Tripathi et al. 2013). The occurrence and continuation of genetic variability is an important tool for crop improvement strategies, however, the loss of locally available land race and adapted germplasm resources has rapid and high, which need to be keep in sustainable conditions (Harlan, 1975). A critical estimation of genetic variability is a precondition for promoting crop improvement strategy and adopting appropriate selection systems (Dhanwani et al. 2013). The genetic variability is determined with the help of certain genetic parameters viz: genotypic coefficient of variation, phenotypic coefficient of variation and heritability. For selection, heritability along with genetic advance is more useful than the heritability estimates alone (Johnson et al. 1955; Cholin et al. 2010; Shinde et al. 2010 and Meshram et al. 2013).

Genetic variability is also the basic tools for crop improvement programs as comprises and provides wider scope for selection. The effectiveness of selection is depending on the nature, extent and magnitude of genetic variability present in the given population with the existence of inheritance between parents and offsprings. The variability in the population is largely due to genetic than environmental effect; the possibility of selecting superior genotypes are a prerequisite for obtaining high yield, which is the ultimate expression of various yield-association characters. Therefore, sometimes-direct selection based on high yielding potential could be not effective (Islam and Rasul 1998). Sometimes very difficult to understand proportion of observed variability is heritable or non-heritable i.e. environmental variation affect our selection procedure directly and indirectly. The process of breeding in the population is primarily conditioned by magnitude and nature of interactions of genotype and environment in the given plant characters. Therefore in the present study the components of variance such as phenotypic and genotypic coefficient of variances, broad sense heritability (H^2), narrow sense heritability (h^2), and estimated genetic advance as percent of mean have computed for pod yield and seed-related traits (Shashikumara, Sanjeev, and Venkataravana 2016).

Inbred line population development, selection, and release a new promising cultivars are one of the strategies of crop improvement programs that have been contributed to increase yield and sustainable agricultural technology innovation and development. Many economically important agronomic traits are quantitative in nature. Quantitative genetic studies are usually based on a simplified model that defines the phenotypic value because of the genotypic plus the environmental effect (Allard 1971; Ramalho et al. 2000; Antonio et al. 2012).

The objectives of the present experiment were to estimate narrow sense and broad sense heritability, to estimate genotypic and phenotypic variability, to evaluate genetic advance, to estimate additive, and dominance gene effects from 251 single cross inbred line populations, which have not been reported earlier.

Materials and Methods

Field experimental and plant materials

The present experiment was carried out using 251 RIL populations derived from the cross between silihong (female parent) and black peanut (male parent). The field trial was conducted in Baoding and Handan environments for two consecutive cropping years from 2015 to 2016 in China using randomized complete block design (RCBD). All pod and see-related phenotypic data were collected after harvesting in three repeats.

Statistical analysis

All pod and seed-related phenotypic data were subjected to system analysis software (SAS ver. 9.4, SAS Institute, USA) using PROC GLM and PROC MIXED model applied for phenotypic variance component analysis in the 251 RIL populations with the included of two parents. Genetic variance component statistical analysis was computed using Plant Breeding Tools version 1.4 software (IRRI, 2014), using single environment analysis system in the restriction maximum likelihood (REML) model and North Carolina one (NC-I) mating design.

Estimation of phenotypic and genotypic variability

Parents and offspring phenotypic and genotypic variances were estimated using the statistical formula developed by Singh, R.K. and Chaudhary, B.D (1979) and the expected mean squares under the assumption of random and fixed effect model was calculated from linear combinations of phenotypic and genotypic coefficient of variations, which were computed as per the methods suggested by Burton and Devane (1953).

$$\text{Genotypic variance } (\sigma^2_g) = \frac{M_{sg} - M_{se}}{r}$$

$$\text{Environmental variance } (\sigma^2_e) = M_{se}$$

$$\text{Phenotypic variance } (\sigma^2_p) = \sigma^2_g + \sigma^2_e$$

Where; M_{sg} and M_{se} are the mean sum squares of the genotypes and error in the analysis of variances respectively r is the number of replications.

Estimation of genotypic and phenotypic coefficient of variability

Genotypic and phenotypic coefficient of variability was computed as per the methods given by Burton and Devane (1953).

- i) Genotypic coefficient of variability (GCV): $GCV = \frac{\sigma^2_g}{\bar{x}} \times 100$
- ii) Phenotypic coefficient of variability (PCV): $PCV = \frac{\sigma^2_p}{\bar{x}} \times 100$

Where,

σ^2_g = Genotypic standard deviation

σ^2_p = Phenotypic standard deviation

$\bar{x}$ = Grand mean of the traits

GCV and PCV values were categorized as low, moderate and high as indicated by Siva Subramanian and Menon (1973). It categorized as follows: 0-10 % low, 10-20 % moderate, and ≥ 20 % high

A. Broad Sense Heritability (H^2)

Broad sense heritability was computed as the ratio of genetic variance to the total phenotypic variance as suggested by Hanson et al. (1956) and expressed as in percentage.

$$\text{Heritability } (H^2) = \frac{\sigma^2_g}{\sigma^2_p} \times 100$$

Where σ^2_g = Genotypic variance and σ^2_p = Phenotypic variance. The heritability percentage have been categorized as low (0-30%), moderate (30-60%), and high ($\geq 60\%$) as developed and given by Robinson et al. (1949).

B. Narrow sense heritability (h^2)

Narrow sense heritability (h^2) was estimated from parent offspring regression analysis according to the method of Anderson et al. (1991).

$$Y = a + bxi + ei \quad \text{Where } e_i = \text{error and } b = \frac{\sigma_{xy}}{\sigma^2_x}$$

Where σ_{xy} = covariance of parent-offspring analysis and σ^2_x = total variance of parental measurements. Genetic correlation between offspring's or RIL population with parental traits determined according to the method suggested and given by Kwon and Torrie (1964):

$$rg = \frac{\text{Cov}_{ij}}{(\sigma^2_{gi} \times \sigma^2_{gj})}$$

Cov_{ij} and σ^2_{gj} are the estimates of covariance and variance for traits i and j.

$$\text{Heritability } (h^2) = \frac{\sigma^2_a}{\sigma^2_p} \times 100$$

Where σ_a^2 = Additive variances and σ_p^2 = Phenotypic variances

Estimated genetic advance

Genetic advance under selection was suggested and estimated using the formula given by (Johnson *et al.* 1955).

$$EGA = H^2 k \sigma_p$$

Where, H^2 = Heritability in broad sense

k = Selection differential which is equal to 2.06 at 5% selection intensity (Lush, 1949).

σ_p = Phenotypic standard deviation.

Genetic advance as percent of mean

Genetic advance as percent of mean has calculated according to the formula given by (Johnson *et al.* 1955).

$$GAM = \frac{GA}{X} \times 100$$

Where, GA= Genetic advance, and X = General mean of the characters/traits

Genetic advance as percent of mean was categorized as low, moderate and high as given by (Johnson *et al.* 1955). It described, as 0-10% low; 10-20% moderate and $\geq 20\%$ high.

Result and discussion

Genotypic and phenotypic variability

The two basic requirements of plant breeding are the presence of genetic variation and exploitation of the existed variation through the method of selection. The presence of genetic variation in a character is necessary for any improvement in that character. Selection is the second basic step in crop improvement breeding programs. Selection involves in the identification and isolation of desirable plants from a vast and variable population. The progeny from selected plants may be released as a variety if they are found suitable and superior to the existing varieties and controls in yield and other important parameters to full fill the requirements of consumers or farmers need. Selection of plants from a population is usually based on their phenotypic performance.

Phenotypic variation has both heritable and non-heritable components that included environmental effects. Moreover, heritable component is due to the genes present in the existed plant population. One or groups of economically important gene(s) mainly control the development of quantitative and qualitative traits. However, the genes cannot able to produce characters directly. In the present study, the highest genotypic coefficient of variation ($>10\%$) was found in the traits of pod length (22.47), number of pods

per plant (23.66), pod weight per plant (28.43), multi-seedpods per plant (30.44), and moderate genetic variation was recorded in the traits of seed weight per plant (19.04). The highest phenotypic coefficient of variation (>10%) had been scored in the traits of pod number per plant (23.99), pod length (25.40), seed weight per plant (29.75), multiple seedpods per plant (30.44), pod weight per plant (41.29). In the previous studies similar findings have been reported on genotypic and phenotypic coefficient of variability in pod and seed related traits such as Shashikumara et al (2016) reported that high GCV and PCV found in pod and seed-related yields traits, such as pod yield, kernel yield, matured pods and oil yield per plant (Lal et al. 2003; Golakia et al. 2005; and Veeramani et al. 2005). Therefore, our selection focused on superior transgressive populations based on their high to moderate genetic advance, heritability and phenotypic variation values.

Analysis of phenotypic variances for pod and seed-related traits

In the present study, we have used 251 RIL populations with two parents as a check for phenotyping in pod and seed-related agronomic traits in two tested environments for testing genetic and phenotypic variations and confirming the expected null hypothesis (H_0) through F-test statistics. The statistical procedures were computed in the combined estimation of analysis of variances from pod and seed-related traits across environments and within consecutive cropping seasons. Based on system analysis software (SAS ver. 9.0) variance analysis matrix of F-calculated statistics result the null hypothesis (H_0) was rejected in the reason of significance mean difference between RIL populations and within environments in the traits of pod length at $P \leq 0.05$ level of significance, that means F-calculated greater than F-tabulated (P-value). Besides the remaining source of variations in the trait of pod, length showed that non-significance difference between treatments that means the F-test of the null hypothesis was accepted. The traits of pod width, pod thickness, pod length by width, thickness of pod shells and multiple-seed pods per plant showed that there was a significance difference between treatments, within environments and some traits expressed differences within years/seasons.

Table 1 GxE combined analysis of variances for Pod traits in the RIL population across two environments

Pod-related traits	Source of Variations	df	MS	F-value	P-value
Pod length (mm)	RIL	252	84.82	3.69	<.0001
	Env	1	162.25	7.05	0.0009
	Year	1	14.50	0.63	0.5327
	RIL x Env	252	38.99	1.32	0.61
	RIL x Yr	450	14.07	0.47	0.85

	Error	702	23		
Pod width (mm)	RIL	252	7.20	2.52	<.0001
	Env	1	65.63	22.94	<.0001
	Year	1	79.32	27.73	<.0001
	RIL x Env	252	4.10	6.79	0.29
	RIL x Yr	450	2.17	3.59	0.4022
	Error	702	2.86		
Pod thickness (mm)	RIL	252	7.74	2.48	<.0001
	Env	1	20.14	6.45	0.0017
	Year	1	3.08	0.99	0.3734
	RIL x Env	252	4.53	906.95	0.0265
	RIL x Yr	450	2.34	469.39	0.0368
	Error	702	3.12		
Pod length by Width (mm)	RIL	252	0.52	4.08	<.0001
	Env	1	0.43	3.34	0.0362
	Year	1	3.82	29.61	<.0001
	RIL x Env	252	0.25	0.63	0.7913
	RIL x Yr	450	0.058	0.14	0.9913
	Error	702	0.13		
Thickness of pod shells (mm)	RIL	252	0.16	1.38	0.0054
	Env	1	2.41	20.57	<.0001
	Year	1	14.41	122.88	<.0001
	RIL x Env	252	0.05	0.43	1.0000
	RIL x Yr	450	0.05	0.42	1.0000
	Error	702	0.12		
Number of pods per plant (No)	RIL	252	46.24	1.11	0.2126
	Env	1	56.19	1.34	0.2475
	Year	1	404.55	9.67	0.0021
	RIL x Env	252	26.16	0.63	0.9999
	RIL x Yr	450	24.55	0.59	1.0000
	Error	702	41.82		
Multiple-seed pods plant (No)	RIL	252	3.10	1.54	0.0003
	Env	1	0.31	0.16	0.6929
	Year	1	39.47	19.59	<.0001
	RIL x Env	252	1.13	0.56	1.0000
	RIL x Yr	252	1.03	0.51	1.0000
	Error	702	2.01		
Pod weight per plant (g)	RIL	252	48.30	1.09	0.2372
	Env	1	900.64	20.41	<.0001
	Year	1	316.83	7.18	0.0079
	RIL x Env	251	28.13	0.64	0.9998
	RIL x Yr	450	23.67	0.54	1.0000
	Error	702	44.14		

For seed related-trait analysis of variances results shown that there were a mean difference between treatments and within environments at $P \leq 0.05$ percentage level of significance in the trait of seed length, seed width, seed thickness. Some seed related traits like seed weight per plant and shelling percentage cannot express mean differences between treatments that indicated the null hypothesis was accepted.

Table 2 GxE Combined analysis of variances (ANOVA) for seed traits in the RIL population

Seed-related traits	Source of Variations	df	MS	<i>F-value</i>	<i>P-value</i>
Seed length (mm)	RIL	252	10.21	2.87	<.0001
	Env	1	109.19	30.69	<.0001
	Year	1	0.005	0.00	0.9984
	RIL x Env	251	4.78	0.52	0.8343
	RIL x Yr	450	2.86	0.31	0.9270
	Error	702	9.24		
Seed width (mm)	RIL	252	1.70	1.67	<.0001
	Env	1	36.00	35.13	<.0001
	Year	1	5.72	5.59	0.0039
	RIL x Env	251	1.14	57.45	0.1049
	RIL x Yr	450	0.95	47.89	0.1148
	Error	702	0.02		
Seed thickness (mm)	RIL	252	1.26	1.69	<.0001
	Env	1	45.15	60.33	<.0001
	Year	1	9.71	12.98	<.0001
	RIL x Env	251	0.83	10.38	0.2435
	RILx Yr	450	0.70	8.80	0.2638
	Error	702	0.08		
Seed length/width (mm)	RIL	252	0.13	2.55	<.0001
	Env	1	0.11	1.98	0.1393
	Year	1	0.29	5.43	0.0046
	RIL x Env	251	0.10	1.26	0.6262
	RIL x Yr	450	0.03	0.36	0.9026
	Error	702	0.08		
Seed weight/plant (g)	RIL	252	21.65	1.04	0.3667
	Env	1	482.59	23.27	<.0001
	Year	1	57.84	2.79	0.0961
	RIL x Env	251	12.58	0.61	1.0000
	RIL x Yr	450	11.81	0.57	1.0000
	Error	702	20.74		
Shelling percentage (%)	RIL	252	108.23	1.00	0.4958
	Env	1	58.01	0.54	0.4645
	Year	1	1532.14	14.17	0.0002
	RIL x Env	251	50.77	0.47	1.0000
	RIL x Yr	450	41.79	0.39	1.0000
	Error	702	108.09		

The comparison of pod and seed-related traits across two environments

The pod and seed-related traits generated from Baoding and Handan environments were shown slight difference between environments, so this result indicated that most of agronomic traits had stability performance and environments effect was less. According to (Nucci, Narvaez, and Krettenauer 2014) the simple standard deviation or coefficient of variation values (CV) indicated that the degree of a good index

of reliability or the precision of the experiments and controlling of experimental errors. The cv can be expresses the experimental errors as the percentage of its means, that means the higher the cv value the less reliability of the experiment. As many field experiment experiences in from different researchers and scientists in different part of the world, the acceptable cv values ranging from 0-6 percent for variety development trials, 10-12 percent for fertilizer trials and 13-15 percent for pesticide and herbicide trials, meanwhile sometimes our cv values depends on the agronomic traits behavior and the situation of the experimental places so in the present study our cv values had a good precision and reliability across the two tested environments, however the cv values Baoding was a little bit greater than in Handan. According to the standardization of cv values for crop breeding programs our cv values in Baoding was ranging from 2.04-19.80 percent and Handan ranged from 3.58-10.56 percent. The relative coefficient of correlation determination R-squared (R^2) values (0 to 1) in pod and seed related traits indicated that in Baoding except pod length by pod width and seed length by seed width traits the remaining traits showed strong correlation values ($R^2 > 0.75$) with dependent and independent variables, in Handan pod length by pod width and pod length traits shown less relative determination correlation values, but the remaining pod and seed-related traits expressed strong correlation indexing values (table 9). So, when compared two locations data the trait pod length by pod width had very low relative correlation determination value. In Baoding the traits of pod length, seed length and seed thickness had expressed perfect correlation determination r-squared values ($R^2 > 0.95$) than other traits, meanwhile in Handan only seed length had perfect correlation determination value ^[168]. The trait seed length had scored highest relative determination values across Baoding (0.99) and Handan (0.96) environments, this indicates this trait had good stability and promising performance and it did not affected by environmental variations (table 10).

Table 3 Descriptive statistical analysis of phenotypic traits of RILs with parents in two environments

Environment	Traits	P1	P2	Range	Mean	SD	LSD	CV	R^2
Baoding	PL	33.9	39.0	32.3-40.3	36.45	3.02	2.61	2.04	0.97
	PWD	13.5	15.8	13.4-17.0	14.66	1.52	3.20	6.21	0.85
	PT	13.4	15.7	13.0-16.2	14.60	1.34	2.24	4.36	0.90
	PLW	2.53	2.50	2.4-2.7	2.51	0.13	0.71	8.11	0.05
	SL	13.8	19.0	12.4-20.5	16.43	3.06	1.41	2.44	0.99
	SWD	8.0	8.9	6.8-11.1	8.50	1.50	3.86	12.95	0.78
	ST	7.4	8.4	6.7-9.3	7.93	0.96	1.03	3.71	0.96
	SLW	1.7	2.2	1.7-2.8	1.96	0.42	1.36	19.80	0.66
Handan	PL	34.2	33.2	33.2-34.2	33.7	0.70	5.04	6.26	0.73
	PWD	12.8	14.4	12.8-14.4	13.6	1.13	1.77	5.47	0.87
	PT	13.2	15.6	13.2-15.6	14.4	1.69	1.17	3.58	0.93
	PLW	2.7	2.3	2.3-2.7	2.5	0.28	0.42	8.47	0.20

SL	13.4	16.3	13.4-16.3	14.8	2.05	1.92	5.33	0.96
SWD	8.1	9.3	8.1-9.3	8.7	0.84	2.03	10.56	0.79
ST	7.2	8.9	7.2-8.9	8.0	1.20	0.73	4.12	0.94

PL pod length, **PWD** pod width, **PT** pod thickness, **PLW** pod length by width ratio, **SL** seed length, **SWD** seed width, **ST** seed thickness, **SLW** seed length by width ratio, **P1** parent-1, **P2** parent-2, **SD** standard deviation, **LSD** least significance difference, **CV** coefficient of variation, **R²** R-square

Pearson's correlation analysis

Genotype by environment (GxE) combined Pearson's correlation coefficient values (-1 and +1) from table-10 indicated that majority of the correlation matrix between the pod and seed-related traits were had positive correlations. The trait pod length (PL) positively correlated with seed length (SL), pod length by pod width ration (PLW), pod thickness (PT), pod width (PWD), seed width (SWD), seed thickness (ST), seed length by seed width ration (SLW), thickness of pod shells (TPS), multiple seed number of pods per plant (MSNP) and pod weight per plant (PWP) but it was negatively correlated with shelling percentage per plant (SP). The trait pod width was positively associated with pod thickness, seed length, seed width, seed thickness, thickness of pod shells, pod weight per plant, seed weight per plant but this agronomic trait negatively or indirectly correlated with pod length by width ratio, pod number per plant, multiple seeds pod number per plant and shelling percentage. The trait pod thickness directly correlated with seed length, seed width, seed thickness, the thickness of pod shells, pod weight per plant, seed weight per plant, pod length and pod width, but it was negatively correlated with pod length by width ratio, pod number per plant, multiple seedpod numbers per plant and shelling percentage. The trait pod length by width ratio had directly proportioned with pod length, seed length, and seed length by width ratio, pod numbers per plant, multiple seedpod numbers per plant, pod weight per plant, seed weight per plant and shelling percentage but it was negatively correlated with pod width, pod thickness, seed width, seed thickness and a thickness of pod shells. The seed length phenotypic trait was positively correlated with seed width, seed thickness, seed length by width ratio, thickness of pod shells, pod weight per plant, seed weight per plant, pod length by width ratio, pod thickness, pod width and pod length but this trait was inversely associated with pod number per plant, multiple seedpod number plant and pod shells per plant. Seed width traits positively correlated with seed thickness, thickness of pod shells, pod weight per plant, seed weight per plant, shelling percentage per plant, seed length, pod thickness, pod width and pod length, but it had negative correlation with seed length by width ratio, pod number per plant, multiple seedpod number per plant and pod length by width ratio. The trait seed thickness directly and positively correlated with thickness of pod shells, pod weight per plant, seed weight per plant, shelling percentage, seed width, seed length, pod

thickness, pod width and pod length, despite it was negatively associated with seed length by width ratio, pod number per plant, multiple seedpod number plant and pod length by width. Pod weight per plant directly proportioned to seed weight per plant, seed thickness, seed width, seed length, pod length by width ratio, pod thickness, pod width, pod number per plant, thickness of pod shells and pod length but it had negatively correlated with seed length by width ratio. Seed weight was directly affected and related with pod weight per plant, pod number per plant, thickness of pod shells, seed thickness, seed width, seed length, pod length by width, pod thickness and pod width but it was negatively correlated with seed length by width ratio, regarding to the correlation matrix of phenotypic pod and seed-related traits clearly stated in table-4.

Table 4 GxE Combined Pearson's correlation coefficient analysis of pod and seed-related traits

Traits	PL	PWD	PT	PLW	SL	SWD	ST	SLW	TPS	PNPP	MSNP	PWP	SWP	SP
PL	1													
PWD	0.43 ^a	1												
PT	0.50 ^a	0.84 ^a	1											
PLW	0.54 ^a	-0.36	-0.19	1										
SL	0.61 ^a	0.59 ^a	0.65 ^a	0.11 ^b	1									
SWD	0.24 ^a	0.63 ^a	0.58 ^a	-0.25	0.51 ^a	1								
ST	0.27 ^a	0.57 ^a	0.54 ^a	-0.17	0.56 ^a	0.66 ^a	1							
SLW	0.24 ^a	0.02	0.08	0.21 ^a	0.30 ^a	-0.23	-0.01	1						
TPS	0.19 ^a	0.53 ^a	0.46 ^a	-0.19	0.30 ^a	0.32 ^a	0.45 ^a	0.25 ^a	1					
PNPP	0.04	-0.12	-0.11	0.13 ^a	-0.12	-0.04	-0.06	-0.08	-0.05	1				
MSNP	0.43 ^a	-0.10	-0.06	0.50 ^a	-0.05	-0.18	-0.14	0.08	-0.10	0.26 ^a	1			
PWP	0.39 ^a	0.27 ^a	0.29 ^a	0.19 ^a	0.27 ^a	0.24 ^a	0.23 ^a	0.03	0.16 ^a	0.76 ^a	0.35 ^a	1		
SWP	0.34 ^a	0.17 ^a	0.19 ^a	0.22 ^a	0.22 ^a	0.26 ^a	0.25 ^a	-0.04	0.08 ^b	0.74 ^a	0.36 ^a	0.95 ^a	1	
SP	-0.11	-0.36	-0.36	0.16 ^a	-0.04	0.19 ^a	0.12 ^a	-0.21	-0.22	0.06	0.07	0.03	0.26 ^a	1

PL= Pod length, **PW**= Pod width, **PT**=Pod thickness, **PLW**=Pod length by width, **SL**=Seed length, **SW**=Seed width, **ST**=Seed thickness, **SLW**=Seed length by width, ^a correlation is significant at **0.01** level, ^bcorrelation is significant at **0.05** level and ^{ns} correlations are non-significant at 0.01 & 0.05 levels.

In the present study high genetic variability were indicated that those RIL populations showed they had genetic variability between them, thus the current variability had similarity with reported by Naazar et al (2000), Singh and Singh (1999), John et al (2006), Kadam et al (2007), and Khote et al (2009) for plant height and pod yield per plant. The highly heritable characters with high genetic advance as percent of mean could be further improved through individual plant selection (John et al 2013). Genetic advance measures the expected genetic progress that would be resulted from selecting the best-performed genotypes for a given characters (Allard, 1960). The genetic gain that can be obtained from a particular trait through selection is the product of its heritability, phenotypic standard deviation and selection differential (Burton and Devane 1953).

Table 5 GxE Combined estimation of genetic advance under selection, genotypic and phenotypic variability, genotypic and phenotypic coefficient of variability, and heritability

Traits	σ^2_g	σ^2_e	σ^2_{er}	σ^2_{yr}	σ^2_p	$\sigma^2_{G \times E}$	GCV	PCV	GA	GAM
PL	7.40	0.97	29.38	0.92	8.37	0.00	22.47	25.40	10.71	32.49
PWD	0.35	0.16	2.50	0.11	0.51	0.00	2.77	4.05	2.31	18.17
PT	0.43	0.20	2.85	0.14	0.63	0.00	3.17	4.65	2.49	18.29
PLW	0.05	0	0.18	0.00	0.05	0.00	2.09	2.09	0.96	36.55
SL	0.69	0.12	3.59	0.20	0.80	0.00	4.54	5.30	3.52	23.26
SWD	0.08	0.05	0.64	0.17	0.13	0.00	1.08	1.73	1.13	14.88
ST	0.06	0.06	0.59	0.04	0.12	0.00	0.78	1.60	0.81	11.23
SLW	0.01	0.00	0.09	0.00	0.01	0.00	0.61	0.62	0.63	30.98
TPS	0.02	0.00	0.08	0.03	0.02	0.00	2.05	2.53	0.54	56.87
PNPP	3.33	0.05	32.91	1.03	3.38	0.00	23.66	23.99	12.02	85.28
MSNP	0.40	0	1.51	0.08	0.40	0.00	30.44	30.44	2.81	215.44
PWP	3.79	1.71	33.13	1.35	5.51	0.00	28.43	41.29	8.66	64.90
SWP	1.64	0.92	15.07	1.29	2.57	0.00	19.04	29.75	5.48	63.49

σ^2_g Genetic variance, σ^2_e Environmental variance, σ^2_{er} Error variance, σ^2_{yr} Year variance, σ^2_p Phenotypic variance, $\sigma^2_{G \times E}$ Genotype by environment interaction variance, **GCV** Genotypic coefficient of variability, **PCV** Phenotypic coefficient of variability, **GA** Genetic advance/genetic gain, and **GAM** Genetic advance as percent of mean. **PL** Pod length, **PWD** Pod width, **PT** Pod thickness, **PLW** Pod length by width, **SL** Seed length, **SWD** Seed width, **ST** Seed thickness, **SLW** Seed length by width, **TPS** Thickness of pod shells, **PNPP** Pod number per plant, **MSNP** Multiple seed number of pods per plant, **PWP** Pod weight per plant, **SWP** Seed weight per plant.

The highest genetic variation was found in the traits of pod length (7.4), pod weight per plant (3.79), number of pods per plant (3.33), and seed weight per plant (1.64). In this experiment the effects of the environment was slightly low however in the traits of pod weight per plant, pod length and seed weight per plant relatively moderate variation than the remaining traits, because the yield is the cumulative effect of many economically important traits. In the present study the highest experimental error have recorded in the traits of pod weight per plant, pod number per plant, pod length, seed weight per plant, seed length, pod thickness and pod width, the rest traits had low experimental errors.

Table 6 The comparative statement of the previously investigated reports of phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) on pod and seed traits

Traits	Components	References
Pod yield	High (PCV)	Raut et al. 2010; Yadlapalli 2014; Patidar et al. 2014; Darvhankar et al. 2016
	Moderate (PCV)	John et al. 2012; Sabiel et al. 2014
	High (GCV)	Raut et al. 2010; Yadlapalli 2014; Patidar et al. 2014
	Moderate (GCV)	Darvhankar et al. 2016
	Low (GCV)	John et al. 2012; Sabiel et al. 2014
Mature pods per plant	High (PCV)	Shoba et al. 2009; Raut et al. 2010; Padmaja et al. 2013b; Nath U.K and Alam(Cui et al. 2020) M.S, 2002 Padmaja et al. 2013a; Yadlapalli 2014; Patidar et al. 2014; Rao et al. 2014; Shashikumara et al. 2016
	Moderate (PCV)	Patil et al. 2014
	High (GCV)	Nath U.K and Alam M.S, 2002; Shoba et al. 2009; Raut et al. 2010; Padmaja et al. 2013a; Yadlapalli 2014; Patidar et al. 2014; Rao et al. 2014; Shashikumara et al. 2016
	Moderate (GCV)	Padmaja et al. 2013b; Patil et al. 2014
Immature pods per plant	High (PCV)	Raut et al. 2010; Padmaja et al. 2013a
	High (GCV)	Raut et al. 2010; Padmaja et al. 2013a

100-pod weight (g)	Moderate (PCV)	Nath U.K and Alam M.S, 2002; John et al. 2013; Patil et al. 2014; Darvhankar et al. 2016
	Moderate (GCV)	Nath U.K and Alam M.S, 2002; John et al. 2013; Patil et al. 2014; Darvhankar et al. 2016
100-seed weight (g)	High (PCV)	Shoba et al. 2009; Padmaja et al. 2013a; Padmaja et al. 2013b
	Moderate (PCV)	John et al. 2013; Yadlapalli 2014; Patil et al. 2014; Rao et al. 2014
	Low (PCV)	John et al. 2011; John et al. 2012; Patidar et al. 2014; Sabiel et al. 2014
	High (GCV)	Shoba et al. 2009; Padmaja et al. 2013a; Padmaja et al. 2013b
	Moderate (GCV)	Shoba et al. 2009; John et al. 2013; Yadlapalli 2014; Patil et al. 2014; Rao et al. 2014
Pod length	Low (GCV)	John et al. 2011; John et al. 2012; Patidar et al. 2014; Sabiel et al. 2014
	High (PCV)	Shoba et al. 2009
	Moderate (PCV)	Shoba et al. 2009
	High (GCV)	Shoba et al. 2009
Pod width	Low (GCV)	Shoba et al. 2009
	Moderate (PCV)	Shoba et al. 2009
	Moderate (GCV)	Shoba et al. 2009
Pod yield per plant	Low (GCV)	Shoba et al. 2009
	High (PCV)	Nath U.K and Alam M.S, 2002; Shoba et al. 2009; John et al. 2013; Padmaja et al. 2013a; Patidar et al. 2014
	Moderate (PCV)	John et al. 2011; Patil et al. 2014; Rao et al. 2014;
	High (GCV)	Nath U.K and Alam M.S, 2002; Shoba et al. 2009; John et al. 2013; Padmaja et al. 2013a; Patidar et al. 2014
Seed yield per plant (g)	Moderate (GCV)	Patil et al. 2014; Rao et al. 2014
	Low (GCV)	John et al. 2011
	High (PCV)	Shoba et al. 2009; Raut et al. 2010; John et al. 2011; John et al. 2012; John et al. 2013; Patidar et al. 2014; Darvhankar et al. 2016
	Moderate (PCV)	Patil et al. 2014; Rao et al. 2014
	Low (PCV)	Patidar et al. 2014
	High (GCV)	Shoba et al. 2009; Raut et al. 2010; John et al. 2013; Patidar et al. 2014
	Moderate (GCV)	Patil et al. 2014; Rao et al. 2014; Darvhankar et al. 2016
	Low (GCV)	John et al. 2011; John et al. 2012; Patidar et al. 2014
Sound mature seeds/plant (%)	High (PCV)	Padmaja et al. 2013a; Padmaja et al. 2013b
	Moderate (PCV)	John et al. 2013; Darvhankar et al. 2016;
	Low (PCV)	John et al. 2011; John et al. 2012; Patidar et al. 2014; Patil et al. 2014;
	High (GCV)	Padmaja et al. 2013a; Padmaja et al. 2013b
	Moderate (GCV)	Darvhankar et al. 2016
	Low (GCV)	John et al. 2011; John et al. 2012; John et al. 2013; Patidar et al. 2014; Patil et al. 2014;
	High (PCV)	Raut et al. 2010
	Moderate (PCV)	Nath U.K and Alam M.S, 2002; Raut et al. 2010; John et al. 2013; Shashikumara et al. 2016; Darvhankar et al. 2016
Shelling (%)	Low (PCV)	John et al. 2011; John et al. 2012; Padmaja et al. 2013a; Padmaja et al. 2013b; Patidar et al. 2014; Patil et al. 2014; Sabiel et al. 2014; Rao et al. 2014
	High (GCV)	Raut et al. 2010
	Moderate (GCV)	Nath U.K and Alam M.S, 2002; Raut et al. 2010; John et al. 2013; Shashikumara et al. 2016
	Low (GCV)	Raut et al. 2010; John et al. 2011; John et al. 2012; Padmaja et al. 2013a; Padmaja et al. 2013b; Patidar et al. 2014; Patil et al. 2014; Sabiel et al. 2014; Rao et al. 2014; Darvhankar et al. 2016
	High (PCV)	Padmaja et al. 2013a
	High (GCV)	Padmaja et al. 2013a
Seed uniformity	High (PCV)	Patidar et al. 2014

Heritability and genetic advance

The quantitative trait inheritance or heritability can be estimated from the given field experiment data on the observed and expected relationship between relatives of the population. The expected resemblance between relatives of the population depends on the assumptions regarding to the characters under environmental and genetic causes.

Robinson et al. (1949) suggested and recommended that the estimated percentage of heritability values of both narrow sense and broad sense have been categorized as low (0-30%), moderate (30-60%), and high ($\geq 60\%$). In the present study the highest narrow sense heritability values were existed in the traits of seed length (66%), pod length by width (87%), and pod thickness (93%), meanwhile the moderate narrow sense heritability values have been scored in multiple seedpods per plant (36%), pod length (47%), and seed length by width (55%), but the rest pod and seed-related traits showed low narrow sense resemblance relations within recombinant populations. In table four as we mentioned many of pod and seed seed-related traits showed low heritability values, in our understanding the iffy causes of this low narrow sense resemblance relative values were; (1) the additive gene effect was very low, (2) non-additive gene action in the pollution were very high, (3) many of pod and seed-related traits were highly subjected to the given environmental variations and genotype by environmental interaction might be high, and (4) perhaps high experimental error plus the inclusive of soil factors and unstable weather conditions. The highest broad sense heritability values had been shown in the traits of seed length (99%), seed length by width (99%), number of pods per plant (95%), shelling percentage (94%), pod thickness (93%), thickness of pod shells (92), seed weight per plant (89%), seed thickness (87%), seed width (83%), multiple seedpods per plant (79%), and pod weight per plant (75%) and the moderate broad sense heritability values found in pod length (47%), but the traits of pod width (2%) had shown very low broad sense and narrow sense heritability values. Some pod traits such as; pod length (47%), pod width (2%), pod length by width (87%), and pod thickness (93) had shown similar narrow sense and broad sense heritability values, this indicates except additive gene effect other gene effects masked and genotype by environment interaction had no significant effect.

According to Johnson et al. (1955) stated that, in our study the highest expected genetic advance selection values or high genetic gain values were existed in the traits of pod length (32.49), seed length (23.26), pod thickness, pod width, multi-seedpods per plant, number of pods per plant, pod weight per plant, seed weight per plant, pod length by pod width ratio, seed thickness. The highest genetic advance

as percent of mean values scored in the traits of multiple seedpods per plant (215.44), number of pods per plant (85.28), pod weight per plant (64.90), seed weight per plant (63.49), thickness of pod shells (56.87), pod length by width (36.55), seed length by width (30.98), seed length (23.26), in addition moderate genetic advance as percent of means have been found in pod thickness (18.29), pod width (18.17), seed width (14.88), and seed thickness (11.23) traits. None of traits had low genetic advance values, so the present study had high genetic gain values.

High heritability combined with high genetic advance was considered as an indication of additive genetic variance (Johanson et al. 1955). However, it has been reported that in many crop including peanut heritability values were highly influenced by the environmental variations (Lin et al. 1971; Singh & Oswalt 1991). In the present study the highest broad sense heritability values coupled with high genetic gain were estimated and identified in the traits of multiple seedpods per plant, number pods per plant, pod weight plant, seed weight per plant, thickness of pod shells, pod length by width, seed length by width, seed length, and some traits had moderate genetic advance as percent of means coupled with high broad sense heritability such as seed width, seed thickness, and pod thickness; similarly in the past other scientists estimated and reported that heritability and genetic advance as percent of mean values from pod and seed related traits in peanut for instance; Shashikumara et al. (2016) were reported in the three inbred line cross high heritability values coupled with high genetic advance as percent of mean, were existed in pod yield, that would be indicated that direct selection applied for pod yield and seed-related traits were more effective in the given populations (Golakia et al. 2005 and John et al. 2013). Similarly Narasimhulu et al (2012) were reported that high broad sense heritability coupled with high genetic advance, as percent mean was existed in pod yield, seed yield per plant and shelling percentage traits. Veeramani et al (2005) were also recorded high broad sense heritability and genetic advance for number of pods per plant and seed yield characters. John et al (2011) were reported high broad sense heritability and genetic advance for harvest index. This indicated that additive gene action plays a vital role for controlling pod and seed-related traits hence individual plant selection would be effective for these pod and seed-related traits. In pod and pod-related traits high genetic gain or genetic advance as percent of mean values reported in number of mature pods per plant, number of immature pods per plant, hundred pod yield, pod yield per plant (Anon et al. 2013) and Shashikumara et al. (2016) they have been also reported that the highest genetic gain was observed in pod traits from three peanut recombinant inbred line populations. For comparison and discussion table two comprised previously investigated heritability values both broad sense and narrow sense.

Table 7 The comparative statement of the past finding reports of heritability (**H**-broad sense and **h**-narrow sense) and genetic advance as percent of mean (**G**) or genetic gain values on pod and seed traits

Traits	components	References
Pod yield	High (H)	Lin et al. 1971; Reddy 1968; Majumdar et al. 1969; Dixit et al. 1970; Sangha 1973b; Patra 1975; Sandhu and Khera 1976; Lakshmaiah 1978; Gibori et al. 1978; Faujdar Singh and D.L. Oswalt 1991; Nath U.K and Alam M.S, 2002; Raut et al. 2010; Jogloy et al. 2011; Padmaja et al. 2013a; John et al 2013; Patidar et al. 2014; Yadlapalli 2014; Shashikumara et al. 2016
	Moderate (H)	Jogloy et al. 2011; Shashikumara et al. 2016
	Low (H)	Bernard 1960; Lin 1966; John et al. 2011; Jogloy et al. 2011; John et al. 2012
	High (h)	Wynne and Rawling 1978; Cahaner 1978
	Moderate (h)	Basu et al. 1986a
	High (G)	Sabiel et al. 2014;Yadlapalli 2014; Patidar et al. 2014; Shashikumara et al. 2016; Darvhankar et al. 2016
Mature pods per plant	Low (G)	John et al. 2012
	High (H)	Kulkarni and Albuquerque 1967; Majumdar et al. 1969; Lin et al.1971; Basu and Ashokraj 1969; Alam et al. 1985; Sandhu and Khera 1976; Sivasubramaniam et al. 1977; Nath U.K and Alam M.S, 2002; Shoba et al. 2009; Raut et al. 2010; Padmaja et al. 2013a; John et al 2013; Patil et al. 2014; Patidar et al. 2014;Yadlapalli 2014; Rao et al. 2014
	High (G)	Dholaria and Joshi 1972; Sangha 1973a; Kushwaha and Tawar 1973; Alam et al. 1985; Nath U.K and Alam M.S, 2002; Shoba et al. 2009; Raut et al. 2010; Padmaja et al. 2013a; Yadlapalli 2014; Patil et al. 2014; Patidar et al. 2014; Rao et al. 2014; Shashikumara et al. 2016; Prabhu et al. 2017
Immature pods per plant	Moderate (G)	Padmaja et al. 2013b
	High (H)	Raut et al. 2010; John et al. 2013; Padmaja et al. 2013a
	High (H & G)	Dholaria and Joshi 1972; Sangha 1973a; Kushwaha and Tawar 1973; Alam et al. 1985
	Low (H)	Lin et al. 1971
	Moderate (h)	John et al. 2011; John et al 2013
100-pod weight (g)	High (G)	Padmaja et al. 2013a
	High (H)	Cahaner 1978; Basu and Ashokraj 1969; Dixit et al. 1970; Nath U.K and Alam M.S, 2002; Patil et al. 2014
	Moderate (H)	John et al. 2013; Darvhankar et al. 2016
	Low (H)	Hammons 1974; Lakshmaiah 1978; Xiang et al. 1984
	High (G)	Nath U.K and Alam M.S, 2002; John et al. 2013; Patil et al. 2014
100-seed weight (g)	Moderate (G)	Darvhankar et al. 2016
	High (H)	Basu and Ashokraj 1969; Dixit et al. 1970; Sangha 1973b; Jogloy et al. 2011; Padmaja et al. 2013a; John et al. 2013; Patil et al. 2014; Rao et al. 2014
	Moderate (H)	Alam et al. 1985; Shoba et al. 2009; Jogloy et al. 2011; Patidar et al. 2014; Yadlapalli 2014
	Low (H)	Shoba et al. 2009; John et al. 2011; Jogloy et al. 2011; John et al. 2012;
	Low (h)	John et al. 2011
	High (G)	Dholaria and Joshi 1972; Sangha 1973a; Kushwaha and Tawar 1973; Badwal et al. 1967; Badwal and Gupta 1968; Shoba et al. 2009; Padmaja et al. 2013a; Padmaja et al. 2013b; Yadlapalli 2014; Patil et al. 2014; Rao et al. 2014
	Moderate (G)	Alam et al. 1985; Shoba et al. 2009; John et al. 2013; Patidar et al. 2014;
	Low (G)	John et al. 2011; Sabiel et al. 2014
	High (H)	Kushwaha and Tawar 1973; Shoba et al. 2009
Pod length	Low (H)	Sibale 1985; Shoba et al. 2009
	High (h)	Wynne and Rawling 1978
	High (G)	Shoba et al. 2009
	Low (G)	Shoba et al. 2009
Pod width	High (H)	Shoba et al. 2009
	Moderate (H)	Shoba et al. 2009
	High (G)	Shoba et al. 2009
	Moderate (G)	Shoba et al. 2009

Pod breadth Seeds per pod	Low (G)	Shoba et al. 2009
	High (H)	Kushwaha and Tawar 1973
	High (H)	Nath U.K and Alam M.S, 2002
Pod yield per plant	Low (H)	Hammons 1974
	High (H)	John et al 2013;Patil et al. 2014; Rao et al. 2014
Seed yield per plant	Moderate (H)	Shoba et al. 2009
	Low (h)	John et al. 2011
	High (G)	Nath U.K and Alam M.S, 2002; Shoba et al. 2009; John et al. 2013; Padmaja et al. 2013a; Patidar et al. 2014; Patil et al. 2014; Rao et al. 2014
	Low (G)	John et al. 2011
	High (H)	Raut et al. 2010; Padmaja et al. 2013a; John et al 2013; Patil et al. 2014; Rao et al. 2014;
	Moderate (H)	Shoba et al. 2009; Darvhankar et al. 2016
	Low (H)	John et al. 2011
Sound mature seeds/plant (%)	High (G)	Shoba et al. 2009; John et al. 2013; Patidar et al. 2014; Patil et al. 2014; Rao et al. 2014; Shashikumara et al. 2016; Darvhankar et al. 2016
	Moderate (G)	Patidar et al. 2014
	Low (G)	John et al. 2011; John et al. 2012
	High (H)	John et al. 2013; Patidar et al. 2014
	Moderate (H)	Patil et al. 2014
	Low (H)	John et al. 2011; John et al. 2012; Darvhankar et al. 2016
	Low (h)	John et al. 2011
Shelling percentage	High (G)	Padmaja et al. 2013a; Padmaja et al. 2013b
	Moderate (G)	John et al. 2013; Shashikumara et al. 2016;Darvhankar et al. 2016
	Low (G)	John et al. 2011; Patidar et al. 2014; Patil et al. 2014
	High (H)	Nath U.K and Alam M.S, 2002;John et al. 2013; Patil et al. 2014; Rao et al. 2014; Darvhankar et al. 2016
	Low (H)	Raut et al. 2010; John et al. 2011; John et al. 2012; Padmaja et al. 2013a
	Low (h)	John et al. 2011
	Moderate (H)	Raut et al. 2010; Patidar et al. 2014
Immature seeds per plant	High (G)	Nath U.K and Alam M.S, 2002; Shashikumara et al. 2016
	Moderate (G)	John et al. 2013; Patidar et al. 2014; Patil et al. 2014; Rao et al. 2014; Darvhankar et al. 2016
	Low (G)	John et al. 2011; Padmaja et al. 2013a; Padmaja et al. 2013b; Sabiel et al. 2014
	High (H)	Padmaja et al. 2013a
Seed uniformity	High (G)	Padmaja et al. 2013a
	High (H)	Patidar et al. 2014
	High (G)	Patidar et al. 2014

Gene effects and genetic variance components

Many researchers have been attempting to identify genetic variability and environmental influences that would be existed in the given population; nevertheless, they may not be in a position to accurate prediction of variations either directly or indirectly only using phenotypic data. However, this situation cannot hamper to evaluate and estimate the relative gene effects and environment variation in the

phenotype variance components. The efficiency of genetic variability can be exploited through selection and it depends upon the heritability of individual characters from the given populations (Bilgin et al. 2010) and it gives an indication of how a given traits would be respond to selection (Falconer and Mackey, 1996).

Anon et al. (2013) were reported the estimation of observed genetic variability is difficult, because it is subjected to environmental variation so due to this reason variance component becomes heritable and non-heritable. The process of breeding in the existed population is primarily conditioned by the magnitude and nature of interactions of genotypic and environmental variations from a given agronomic traits. Moreover, it is important to partition the observed variability into its heritable and non-heritable components and to have an understanding of parameters like genetic coefficient of variation, heritability and genetic advance or genetic gains.

Table 8 Estimated genetic variances based on REML model using North Carolina one (NC-I) mating design and parent offspring regression analysis

Traits	σ^2_A	$\sigma^2_{A \times E}$	σ^2_D	$\sigma^2_{D \times E}$	h^2	H^2	Dr
SL	2.52	0.00	1.32	0.003	66	99	1.02
SWD	0.12	0.13	0.49	0.00	16	83	2.85
SLW	0.05	0.00	0.04	0.00	55	99	1.27
ST	0.15	0.08	0.43	0.00	23	87	2.39
SWP	4.39	1.32	10.08	0.56	27	89	2.14
PL	21.48	0.00	0.00	0.00	47	47	0.00
PWD	0.04	0.00	0.01	0.00	2	2	0.63
PLW	0.24	0.01	0.00	0.02	87	87	0.00
PT	5.76	0.01	0.00	0.39	93	93	0.00
TPS	0.01	0.01	0.08	0.00	8	92	4.62
MSNP	0.72	0.42	0.87	0.00	36	79	1.55
PWP	8.04	10.39	22.84	0.00	19	75	2.38
PNPP	2.02	1.87	31.70	0.00	6	95	5.61
SP	6.39	4.79	63.11	0.00	9	94	4.45

σ^2_A =Additive variance, $\sigma^2_{A \times E}$ =Additive by environment interaction variance, σ^2_D =Dominance variance, $\sigma^2_{D \times E}$ =Dominance by environment interaction variance, h^2 =Narrow sense heritability, H^2 =Broad sense heritability, **Dr**=Dominance ratio. **SL** seed length, **SWD** seed width, **SLW** seed length by width, **ST** seed thickness, **SWP** seed weight per plant, **PL** pod length, **PWD** pod width, **PLW** pod length by width, **PT** pod thickness, **TPS** thickness of pod shells, **MSNP** multiple seedpods per plant, **PWP** pod weight per plant, **PNPP** pod number per plant, **SP** shelling percentage.

In the present study, the highest additive gene effect was existed in the traits of pod length (21.48), pod weight per plant (8.04), shelling percentage (6.39), and pod thickness (5.76), seed weight per plant (4.39), seed length (2.52), and pod number per plant (2.02). The highest dominant gene effect was found in the traits of shelling percentage (63.11), pod number per plant (31.70), pod weight per plant (22.84), seed weight per plant (10.08), and seed length (1.32). Additive gene action/effect interact with the existed environment that had high influence on pod weight per plant (10.39), shelling percentage (4.79), pod

number plant (1.87), and seed weight per plant (1.32); besides the effect of dominance gene action with the interaction of the given environment had not shown significance change in all pod and seed-related traits. Estimation of heritability in the given populations depends on the partition and the association of observed phenotypic variation components into the reflection of unobserved genetic and environmental effects.

Table 9 The level of heredity/inheritance, gene effect, and environmental influences onto the RIL populations

Traits	h^2	H^2	Gene effect		Genetic gain	Env. influence	GxE effect
SL	High	High	Additive	Dominance	High	Low	Very low
SWD	Low	High	Non-additive	Non-dominance	Moderate	Low	Very low
SLW	High	High	Additive	Non-dominance	High	Low	Very low
ST	Low	High	No-additive	Non-dominance	Moderate	Low	Very low
SWP	Low	High	Non-additive	Dominance	High	Moderate	Very low
PL	Moderate	Moderate	Additive	Non-dominance	High	Moderate	Very low
PWD	Low	Low	Additive	Non-dominance	Moderate	Low	Very low
PLW	High	High	Additive	Non-dominance	High	Low	Very low
PT	High	High	Additive	Non-dominance	Moderate	Low	Very low
TPS	Low	High	No-additive	Non-dominance	High	Low	Very low
MSNP	Moderate	High	Additive	Dominance	High	Low	Very low
PWP	Low	High	Non-additive	Dominance	High	Moderate	Very low
PNPP	Low	High	Non-additive	Dominance	High	Low	Very low

SL seed length, **SWD** seed width, **SLW** seed length by width **ST** seed thickness,, **SWP** seed weight per plant, **PL** pod length, **PWD** pod width, **PLW** pod length by width, **PT** pod thickness, **TPS** thickness of pod shells, **MSNP** multiple seedpods per plant, **PWP** pod weight per plant, **PNPP** pod number per plant

In the concept of quantitative genetics, the population structure was understood through the estimation of genetic variance components in the outcomes of allelic and non-allelic gene effects with the included of interaction effects called epistasis. Bateson (1909) has designated the interaction effects alleles from different loci to predicted epistasis allele effects. In the year of 1918, Fisher was attempting to partition the genetic variances components as additive (average effects of genetic alleles), dominant (interaction between alleles of the same locus) and epistatic (interactions between alleles in different loci), of which the latter was considered the most complex for trait inheritance studies (Fisher 1984). According to Bernardo (2002), epistatic effects can be exist when the sum of the individual effects of the loci are larger or smaller than the overall effects therefore; besides in the absence of epistatic effects, a single additive-dominant model would be fully explain the expression of a traits. On the other hand, when epistasis is present, it can bias the estimates of additive and dominant genetic variance components, resulting in inaccurate estimates of important genetic parameters, such as heritability and expected response to selection (Antonio et al. 2012). In the present study the additive gene effects observed in the traits of seed length, seed length by width, pod length, pod width, pod length by width, pod thickness, thickness of pod

shells, and multiple seedpods per plant. For more discussion and comparison, the following table five showed the statement of comparison our findings with previously investigated outcomes by different researchers in different time.

Table 10 Genetic variance components and gene effects on pod and seed-related traits

Traits	Components	Gene effect	Envt. influence	References
Total pods/ plant	High (G)	Additive	Low to moderate	Shashikumara et al. 2016
Matured pods/plant	High (G)	Additive	Low	Shashikumara et al. 2016
Seed yield/plant	High (G)	Additive	Low	Shashikumara et al. 2016
Sound mature seed (%)	Low to high (G)	Additive +Non-additive	Low	Shashikumara et al. 2016
Pod yield/plant (g)	High (G)	Additive	Low	Sridharan and Marappan 1980; Basu et al. 1987; Shashikumara et al. 2016;
		Additive +Non-additive	Low	Mohammed et al. 1978
		Non-additive		Schilling 1986; Sandhu and Khera 1976
Shelling (%)	High (G)	Additive	Low	Shashikumara et al. 2016
Pod number/ plant		Non-additive		Sandhu and Khera 1976; Dwivedi et al. 1989
100 pod weight		Non-additive		Schilling 1986
100 seed weight		Additive		Sridharan and Marappan 1980
		Additive +Non-additive		Reddy et al. 1986
		Non-additive		Sandhu and Khera 1976
Number of seeds/pod		Non-additive		Schilling 1986
Pod length		Additive		Dwivedi et al. 1989
		Non-additive		Schilling 1986
Pod size		Additive +Non-additive		Mohammed et al. 1978
		Non-additive		Schilling 1986

In the present study high narrow sense heritability coupled with high additive gene variance was recorded in pod thickness and seed length traits, pod length by width trait had high narrow sense heritability value but it had low additive genetic variance, moderate narrow sense heritability coupled with high additive genetic variance had been existed in the trait of pod length, this indicates the effect of the gene is additive gene effect, however sometimes this assumption affected by several uncertainty reasons, for instance the variation of the given environment, experimental errors and others, the remaining pod and seed traits had scored low narrow sense heritability values. Therefore, for selection we have been recommended the traits that should have high heritability values coupled with high additive genetic variances.

Conclusion

The highest broad sense heritability values coupled with high genetic gain were estimated in multiple seedpods per plant, number of pods per plant, pod weight plant, seed weight per plant, thickness of pod shells, pod length by width, seed length by width. The present study will be helpful for peanut

improvement programs to harnessing heritability and genetic variability within and between individual populations.

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Conflict of interest

The author declared that no conflict of interests.

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