



RESEARCH ARTICLE

Gene action studies of yield-contributing traits in groundnut (*Arachis hypogaea* L.) through generation mean analysis

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Abstract

Peanuts (*Arachis hypogaea* L.) are a vital leguminous crop that is grown for both their oil and edible seeds. It is essential to research the gene activity of groundnut features that contribute to yield in order to create effective breeding plans that will increase quality and productivity. The current study was performed in *Kharif* 2024 at Department of Oilseeds, Tamil Nadu Agricultural University, Coimbatore. Six parameter generation mean analysis was performed for two crosses, Cross I (VRI 9 × Girnar 5) and Cross II (BSR 2 × Girnar 5), were evaluated with three parental lines: VRI 9, BSR 2 and Girnar 5. Results show that additive and dominance gene actions influence trait inheritance. Additive × additive interaction played a key role in all the traits in both crosses except days to 50 % flowering and single plant yield in cross II. Similarly, additive × dominance interaction influenced days to 50 % flowering, no. of pods per plant, no. of mature pods per plant, shelling percentage and oil content in cross I. Whereas shelling percentage along with test weight in cross II. Dominance × dominance interaction was seen in all the traits except no. of mature pods per plant in cross I and days to 50 % flowering and primary branches of cross II. These results provide important information for comprehending genetic interactions in groundnut breeding projects and for creating practical plans to enhance yield and other agronomic characteristics over the course of multiple generations.

Keywords: climate change; drought; intercropping; salinity; sustainability; tolerance

Introduction

Groundnut (*Arachis hypogaea* L.), the “king of oilseeds” is the third largest oilseed crop produced in the world. The allotetraploid cultivated peanut (AABB, $2n=4x=40$) most likely descended from two diploid species, *Arachis duranensis* (A genome) and *Arachis ipaensis* (B genome), donor, followed by chromosome doubling. Since groundnuts are a nutrient-dense crop that contains 44–56 % oil and 22–30 % protein along with vitamins and minerals, they are also known as the poor man's almond. For farmers in Asia and Africa with limited resources, groundnuts are an essential food and cash crop. Because of its nutritional, therapeutic and fodder qualities, it can be used and consumed in a variety of ways (1). Due to its monophyletic origin, lack of gene flow caused by the ploidy barrier and self-pollination, the groundnut crop has a small genetic base despite its morphological, biochemical and physiological heterogeneity (2). The functional units that control an individual's development of different features are called genes. Plant breeders must have a thorough understanding of gene action, which is defined as the behavior or mode of expression of genes in a genetic population (3). Understanding gene activity in plant breeding aids in the estimate of some other genetic factors, the selection of parents for hybridization programs and the selection of the best breeding

technique for the genetic enhancement of different quantitative traits. There are three types of gene action: additive, dominant and epistatic. Gene action is quantified in terms of genetic variance components.

Since additive genetic variance is the only genetic variable that reacts to selection, it is a prerequisite for genetic gain under selection (4). Numerous quantitative traits in groundnuts have been proposed to be inherited through non-additive variance (dominance and epistasis) in addition to additive variation (5). Even though non-allelic interactions in groundnuts are not widely exploited, groundnut breeders could still benefit from knowing about them in order to create suitable breeding protocols. While the additive kind of epistasis may be helpful because it may be fixed in homozygous cultivars, the variation caused by dominance effects and their interactions cannot be efficiently exploited in crops such as groundnuts (6). For a plant breeder to begin a prudent breeding program, knowledge of the type of gene action underlying the expression of different traits is therefore crucial. Therefore this study focused on identifying the gene interactions for yield and yield contributing traits in two crosses of groundnut.

Materials and Methods

Location and climatic conditions: The research was conducted at the Department of Oilseeds, Tamil Nadu Agricultural University, Coimbatore. The study site was located at 11° N latitude and 77° E longitude and it is 426.72 m above mean sea level. The soil type of the experimental farm is sandy loam and found in a tropical climate with temperatures ranging from 24–34 °C.

Experimental material

Crosses were made between three parents VRI9, BSR2 and Gimar5. F₁ hybrids were developed in *Kharif* 2023 by crossing VRI 9 x Gimar 5 (Cross I) and BSR 2 x Gimar 5 (Cross II). In the following season (*Rabi* 2023) F₁ hybrids of two crosses were raised and crosses were made with the female and male parents to develop the B1 and B2 populations respectively. Simultaneously F₂ seeds were developed by selfing of F₁ plants. For evaluating P₁, P₂, F₁, F₂, B₁ and B₂ generations sowing was done in randomized complete block design with three replications in *Kharif* 2024. Standard agricultural practices were followed per recommended guidelines to ensure healthy crop cultivation.

Observations recorded

Nine traits were recorded from each genotype: Days to 50 % Flowering (DF), Days to Maturity (DM), Primary Branches (PB), No. of Pods per Plant (PPP), No. of Mature Pods per Plant (MPP), Shelling percentage (%) (SH), Test Weight (TW) (g), Single Plant kernel Yield (SPY) (g), Oil Content (OC) (%). In cross I and cross II, nine traits were analyzed.

Statistical analysis

Scaling tests (A, B, C and D) were performed for each trait to evaluate the additive dominance model and detect non-allelic gene interactions, following the approach with the different generations of both crosses (24). Significance was assessed via a t-test, with results considered significant if they deviated from zero within their standard errors. Statistical analyses were performed via MS Excel and the TNAU STAT package (7).

Results

Our findings revealed wide variation in means among the six populations from the two studied crosses (P₁, P₂, F₁, B₁, B₂ and F₂) across most traits (Table 1).

Scaling test

All of the characters in both crosses underwent scaling tests. It will verify whether epistasis for the specific character is present or not. Every attribute, except for DF in cross II, showed significance in the results. To evaluate the gene action for DF in cross II, a three-parameter model is adequate, while a six-parameter model is required to estimate all kinds of interactions for the remaining traits in both crossings (Table 2).

Intra allelic interactions

These are the interactions that exists within the alleles of a gene. Among all the characters of two crosses cross I had shown significant additive effect for the traits like DM (-2.23**), PB (-1.20*), PPP (-7.06**), SH (-3.30**), single plant yield (-3.44**) and OC (-3.82**). Significant dominance effects were seen for all the traits except MPP (3.51), TW (6.92) and yield (0.59). Whereas in cross II significant additive effects were seen for no. of branches per plant (-2.16), PPP (4.6**), MPP (4.33**), TW (-0.99*), single plant yield (0.89*) and OC (-1.78**). Significant dominant effects for days to 50 % flowering (-4.35*), no. of branches per plant (2.52*), MPP (7.68*), SH (20.17**), TW (-5.73**), OC (13.48**) as shown in Table 3.

Inter-allelic reactions

These are the interactions that exist between the alleles. DF has shown all types of interaction namely additive x additive (3.91**), additive x dominance (1.86**) and dominance x dominance (-5.84**) in cross I. In cross II it does not show any type of epistasis indicating additive dominance model of that trait and three parameter model is sufficient to explain the gene action of this trait. DM has shown additive x additive (2.42**) and dominance x dominance (-2.22**) in cross I and cross II additive x additive (2.50**) and dominance x dominance (-4.55**) crosses. No. of branches per plant branches has shown additive x additive interaction in both crosses (3.77** in cross I and 3.23** in cross II) and dominance x dominance (0.04**) in cross I. PPP has shown additive x additive (8.06*), additive x dominance (-12.04**) and dominance x dominance (13.98**) in cross I and additive x additive (-6.00**), dominance x dominance (31.96**) in cross II. No of mature pods per plant has shown additive x additive (4.80**), additive x dominance (-2.51*) in cross I and additive x additive (4.33**), dominance x dominance (10.03*) in cross II. SH has shown all types of interactions in both crosses. In cross I additive x additive (7.90**), additive x dominance (-2.39**) and dominance x dominance (-7.78*) while, additive x additive (20.66**), additive x

Table 1. Mean performance and standard error of yield-contributing traits in six populations of groundnut in two crosses

| Character | Cross | P ₁ | P ₂ | F ₁ | F ₂ | B ₁ | B ₂ |
|------------------------------|-------|----------------|----------------|----------------|----------------|----------------|----------------|
| Days to 50 % flowering | I | 28.00± 0.45 | 30.08 ± 0.42 | 29.83± 0.37 | 29.12 ± 0.15 | 30.33 ± 0.46 | 29.86 ± 0.47 |
| | II | 31.10 ± 0.48 | 30.08 ± 0.42 | 29.30± 0.36 | 30.50 ± 0.28 | 29.60 ± 0.36 | 30.06 ± 0.46 |
| Days to maturity | I | 104.15 ± 0.20 | 108.05 ± 0.29 | 107.56± 0.25 | 106.17 ± 0.11 | 105.66 ± 0.24 | 107.90 ± 0.25 |
| | II | 108.30 ± 0.4 | 108.05 ± 0.29 | 107.16 ± 0.21 | 107.55 ± 0.15 | 107.96 ± 0.25 | 108.40 ± 0.22 |
| No. of branches | I | 8.65 ± 0.31 | 9.50± 0.35 | 8.63 ± 0.16 | 6.82 ± 0.14 | 7.16 ± 0.29 | 8.36 ± 0.44 |
| | II | 6.05 ± 0.19 | 9.50± 0.35 | 7.06 ± 0.24 | 7.04 ± 0.18 | 6.76 ± 0.27 | 8.93 ± 0.36 |
| No. of pods per plant | I | 34.00 ± 0.48 | 29.05 ± 0.99 | 35.06 ± 0.40 | 27.01 ± 0.37 | 32.50 ± 0.93 | 27.56 ± 1.67 |
| | II | 35.65 ± 0.76 | 29.05 ± 0.99 | 36.00 ± 0.33 | 29.83 ± 0.64 | 31.13 ± 0.57 | 28.13 ± 1.14 |
| No. of mature pods per plant | I | 19.90 ± 0.42 | 18.80 ± 0.68 | 23.23 ± 0.39 | 16.25 ± 0.30 | 16.46 ± 0.48 | 18.43 ± 1.11 |
| | II | 24.70 ± 0.71 | 18.80 ± 0.68 | 25.10 ± 0.44 | 18.75 ± 0.51 | 22.00 ± 0.78 | 17.66 ± 0.68 |
| Shelling % | I | 69.68 ± 0.23 | 71.48 ± 0.60 | 67.30 ± 0.37 | 66.93 ± 0.37 | 67.26 ± 0.45 | 70.56 ± 0.63 |
| | II | 70.11 ± 0.93 | 71.48 ± 0.60 | 70.32 ± 0.66 | 62.82 ± 0.66 | 67.92 ± 0.76 | 68.06± 0.81 |
| Test weight (g) | I | 44.47 ± 0.32 | 40.55 ± 0.24 | 41.07 ± 0.29 | 38.97 ± 0.62 | 41.99 ± 0.19 | 40.13 ± 1.32 |
| | II | 41.78 ± 0.22 | 40.55 ± 0.24 | 42.09 ± 0.18 | 43.25 ± 0.44 | 41.08 ± 0.34 | 42.08 ± 0.21 |
| Single plant yield (g) | I | 16.30 ± 0.22 | 16.49 ± 0.58 | 16.80 ± 0.94 | 13.05 ± 0.26 | 14.33 ± 0.59 | 15.04 ± 0.50 |
| | II | 18.20 ± 0.19 | 16.49 ± 0.58 | 19.18 ± 0.63 | 13.80 ± 0.37 | 17.08 ± 0.30 | 15.23 ± 0.36 |
| Oil content (%) | I | 44.11 ± 0.27 | 48.23 ± 0.17 | 45.06 ± 0.35 | 42.73 ± 0.15 | 42.88 ± 0.26 | 46.71 ± 0.42 |
| | II | 43.71 ± 0.32 | 48.32 ± 0.17 | 45.24 ± 0.38 | 41.30 ± 0.37 | 43.97 ± 0.38 | 45.76 ± 0.37 |

Table 2. Scaling test for adequacy of additive and dominance model

| Character | Cross | Scaling test | | | |
|------------------------------|-------|--------------|----------|----------|----------|
| | | A | B | C | D |
| Days to 50 % flowering | I | 2.833* | -0.99 | -1.98 | -1.95** |
| | II | -1.20 | 0.33 | 1.53 | 1.35 |
| Days to maturity | I | -0.38 | 0.18 | -2.62** | -1.21** |
| | II | 0.46 | 1.58** | -0.45 | -1.25** |
| No. of branches | I | -2.68** | -1.13 | -7.59** | -1.88** |
| | II | 0.41 | 1.30 | -1.51 | -1.61** |
| No. of pods per plant | I | -23.06** | 1.01 | -30.11** | -4.03 |
| | II | -13.38** | -12.78** | -19.96** | 3.00** |
| No. of mature pods per plant | I | -5.03** | 0.01 | -9.83** | -2.40 |
| | II | -5.80** | -8.56** | -18.70** | -2.16** |
| Shelling % | I | -2.45* | 2.34 | -8.01** | -3.95** |
| | II | -4.58** | -5.68** | -30.92** | -10.33** |
| Test weight (g) | I | -1.55* | -1.36 | -11.27** | -4.17* |
| | II | -1.69* | -1.51** | 6.47** | 3.32** |
| Single plant yield (g) | I | -9.59** | -3.92* | -9.99** | 1.76* |
| | II | -6.63** | -7.35** | -12.73** | 0.63 |
| Oil content (%) | I | -3.14** | 0.03 | -11.65** | -4.13** |
| | II | -1.01 | -2.04** | -17.31** | -7.12** |

Table 3. Genetic components of generation mean for the two crosses

| Character | Cross | Genetic parameters | | | | | |
|------------------------------|-------|--------------------|----------|----------|----------|----------|----------|
| | | <i>m</i> | <i>d</i> | <i>h</i> | <i>i</i> | <i>j</i> | <i>l</i> |
| Days to 50 % flowering | I | 29.12** | 0.46 | 4.32** | 3.91** | 1.86* | -5.84* |
| | II | 30.58** | -0.46 | -4.35* | -2.70 | -0.61 | 3.8 |
| Days to maturity | I | 106.17** | -2.23** | 3.89** | 2.42** | -0.28 | -2.22** |
| | II | 107.55** | -0.43 | 1.49 | 2.50** | -0.55 | -4.55** |
| No. of branches | I | 6.82** | -1.20* | 3.06* | 3.77** | -0.77 | 0.04 |
| | II | 7.04** | -2.16** | 2.52* | 3.23** | -0.44 | -0.49 |
| No. of pods per plant | I | 27.01** | -7.06** | 9.11* | 8.06* | -12.04** | 13.98** |
| | II | 29.93** | 4.6** | -3.85 | -6.00** | -0.20 | 31.96** |
| No. of mature pods per plant | I | 16.25** | -1.96 | 3.51 | 4.80** | -2.51* | 0.23 |
| | II | 18.75** | 4.33** | 7.68* | 4.33** | 1.38 | 10.03* |
| Shelling % | I | 66.93** | -3.30** | 4.62* | 7.90** | -2.39** | -7.78* |
| | II | 62.82** | -0.13 | 20.17** | 20.66** | 3.54** | -10.39** |
| Test weight (g) | I | 38.97** | 1.86 | 6.92 | 8.32* | -0.09 | -5.43* |
| | II | 43.25** | -0.99* | -5.73** | -6.65** | -1.60* | 6.48** |
| Single plant yield (g) | I | 13.05** | -3.44** | 0.59 | -3.53* | -2.83** | 17.06** |
| | II | 13.80** | 0.89* | 3.13 | -1.26 | 0.35 | 15.26** |
| Oil content (%) | I | 42.73** | -3.82** | 7.12** | 8.26** | -1.72** | -4.88* |
| | II | 41.30** | -1.78** | 13.48** | 14.25** | 0.51 | -11.20** |

dominance (3.54**) and dominance x dominance (-10.39**) in cross II. TW has shown all types of interactions in cross II, additive x additive (-6.65**), additive x dominance (-5.43**) and dominance x dominance (6.48**) and additive x additive (8.32*), dominance x dominance in cross I. Single plant yield has shown additive x additive (-3.53*), additive x dominance (-2.83**), dominance x dominance (-17.06**) in cross I and dominance x dominance (15.26**) in cross II. OC has shown all types of interactions additive x additive (8.26**), additive x dominance (-1.72**), dominance x dominance (-4.88**) in cross I and additive x additive (14.25**), dominance x dominance (-11.20**) in cross II.

Discussion

By comprehending the relationship between yield and its constituent parts, genetic analysis of quantitative traits primarily through Generation Mean Analysis (GMA) allows for accurate genetic variance partitioning and aids in breeding program optimization (8). Breeding tactics for crop improvement are influenced by non-allelic interactions or epistasis, which contribute significantly to genetic variance (9,10). Understanding the gene action behind a trait's expression is necessary to improve it. Gene action is estimated using a variety of biometric techniques, including the line x tester, diallel,

partial diallel, GMA and Triple Test Cross (TTC). Only GMA and TTC evaluate nonallelic interactions among them. Although TTC detects if epistasis is present or not, it does not quantify its constituent parts.

GMA, on the other hand, assesses both the existence of epistasis and the size of its constituent parts (11). To provide insights for breeding high-yielding groundnuts with improved OC, this study examines gene action in groundnut populations with an emphasis on yield attributes and OC. Hayman's six-parameter model (12) was used to perform GMA to evaluate epistatic effects from two crosses. This all-encompassing strategy seeks to advance knowledge of the genetic variables affecting groundnut characteristics, which will aid in the creation of superior cultivars. In plant breeding, gene action is essential because it allows breeders to assess parental potential, maximize hybrids, use heterosis and additive effects to increase robustness and yield (8,9).

The significant dominance effects, along with additive x additive, dominant x dominant and additive x dominant interactions, suggest that both additive and non-additive genetic components influence the DF in groundnut. Dominance effects indicate that heterozygous individuals may exhibit varying flowering times, while additive x additive interactions highlight the importance of cumulative allele effects. The presence of dominant x dominant

and additive \times dominant interactions suggests complex inheritance patterns. For long-term breeding in self-pollinated species, emphasis should be placed on additive gene effects, while considering non-additive effects for early-generation hybridization. Similar results were reported by (13). For DM presence of dominant effects suggests that heterozygous individuals may show varying maturity times, while additive \times additive and dominant \times dominant interactions imply complex genetic interactions influencing this trait in cross I. In cross II, only additive \times additive and dominant \times dominant interactions are significant. These findings suggest that for both hybridization and selection for additive effects could be beneficial for achieving desirable maturity.

For PB in cross I, where both additive and non-additive effects (dominant \times dominant and additive \times additive interactions) are significant. Suitable breeding strategy would involve hybridization to exploit dominant effects and heterosis in early generations, followed by selection for additive effects in later generations to ensure stable inheritance of the trait. For cross II, where additive effects and dominant effects are significant, the breeding strategy should focus on selecting parents with desirable additive alleles and dominant effects to improve the trait, utilizing self-pollination and selection to stabilize the desirable traits over multiple generations (14). Similarly, PPP where significant additive, dominant effects and all types of epistasis (additive \times additive, dominant \times dominant and additive \times dominant) are observed, the breeding strategy should focus on hybridization to capture heterosis and dominant gene effects followed by selection for additive effects in subsequent generations (15). The presence of epistasis suggests the need for multi-locus selection to account for gene interactions. This approach would help in improving the trait with more predictable inheritance patterns over generations (16).

For MPP in cross I, with significant additive \times additive and additive \times dominant interactions the breeding strategy should focus on selecting additive gene effects while also considering dominant \times additive interactions to improve pod number. Hybridization could be useful for exploiting both additive and dominance effects in early generations. In cross II, where additive, dominant effects and both additive \times additive and dominant \times dominant interactions are significant, the strategy should involve hybridization for capturing the heterosis and selection in later generations similar study reported by (17). For Cross 1, where additive, dominant effects and all types of epistasis (additive \times additive, additive \times dominant and dominant \times dominant) are significant for SH, the breeding strategy should focus on hybridization to capture the dominant effects and heterosis in early generations. In later generations, you can select for additive effects to stabilize the trait. The significant epistasis suggests that multi-locus selection for cross II, where dominant effects and all types of epistasis are significant, the strategy should focus on selecting for dominant gene effects along with understanding the epistatic interactions similar study was reported by (18). Since all epistasis types are significant, incorporating gene interactions into the selection process is crucial for improving SH over generations (19).

In cross I, where additive \times additive and dominant \times dominant interactions are significant for TW, the breeding strategy should focus on selection for additive effects while also considering dominant \times dominant interactions. This combination suggests that additive and dominance effects are influencing the trait and the focus should be on stabilizing additive effects and utilizing the

dominant effects in the early generations. For cross II, where additive, dominant effects and all types of epistasis are significant, the strategy should prioritize selection for both additive and dominant effects while considering the epistatic interactions (additive \times additive, additive \times dominant and dominant \times dominant). This approach will help capture the complex genetic interactions affecting TW, ensuring improvements over multiple generations similar study was reported by (20).

For cross I, where additive effects and all types of epistasis are significant for single plant yield, the breeding strategy should focus on selection for additive effects and consider epistatic interactions to capture the combined effects of gene interactions. Gene pyramiding or multi-locus selection would help improve yield by targeting these complex gene interactions. For cross II, where only additive effects and dominant \times dominant interactions are significant, the breeding strategy should prioritize selection for additive effects and consider the dominant \times dominant interactions to improve yield, a similar observation was reported in an earlier study (21). This approach will ensure more predictable and stable improvements in the trait over generations.

For cross I, where additive effects, dominant effects and all types of epistasis are significant for OC, the breeding strategy should focus on hybridization to exploit dominant effects in the early generations and selection for additive effects in later generations. The significant epistatic interactions suggest the need for multi-locus selection to capture complex gene interactions for improving OC. For cross 2, where additive and dominant effects and additive \times additive and dominant \times dominant interactions are significant, the strategy should focus on selecting for both additive and dominant effects while considering the additive \times additive and dominant \times dominant interactions (16). This approach will help improve OC by leveraging both types of genetic effects and interactions effectively.

Conclusion

The gene action influencing yield-attributing traits in groundnut (*Arachis hypogaea* L.) is complex, involving a combination of additive and dominance effects. Both additive and dominance gene actions were observed in the inheritance of key traits, with interactions between these gene actions playing significant roles in the expression of traits such as DF, number of pods per plant and OC. Notably, the additive \times additive interaction was found to be crucial in most traits across both crosses, except for DF and single plant yield in Cross II. The dominance \times dominance interactions were also significant, affecting nearly all traits, except for a few specific traits like the MPP in cross I and DF in cross II. This highlights the importance of considering both additive and dominance gene effects, as well as their interactions, when formulating breeding strategies. Prioritizing additive gene effects is crucial for long-term breeding in self-pollinated crops like groundnuts, but non-additive interactions need also be taken into account. The relevance of multi-locus selection, which takes gene interactions into account and produces more stable and predictable genetic gains, is highlighted by the notable epistasis seen across a number of phenotypes. Achieving desired results and improving these qualities over the course of multiple generations will need breeding strategies that are particular to the genetic impacts and interactions of each attribute.

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Authors' contributions

All authors contributed equally to the preparation of manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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