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Morphological traits governing drought tolerance in groundnut (*Arachis hypogaea* L.): A multi-generational evaluation

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Abstract
Drought stress induces substantial variation in key morphological traits that determine yield potential and adaptation strategies in groundnut. Understanding the inheritance of these traits across generations is essential for identifying suitable breeding strategies aimed at improving drought-tolerant cultivars. This study evaluated nine morphological traits *viz.*, days to 50 percent flowering, days to maturity, number of branches per plant, number of mature pods per plant, haulm yield per plant, dry pod yield per plant, hundred kernel weight, shelling percentage and harvest index on dry weight basis, across six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) under irrigated and drought-stress conditions. The data obtained were subjected to generation mean analysis to assess the nature and magnitude of gene effects. The analysis of variance revealed significant differences among all six generations for all the traits studied under both irrigated and drought conditions, indicating the presence of considerable variability in the material assessed. F_1 means were generally intermediate or exceeded the better parent, suggesting incomplete dominance for several traits. Under irrigated conditions, TAG-24 exhibited superiority for yield-related traits, while the drought-tolerant parent ICG 4670 performed better under water stress. F_2 population was superior for dry pod yield under irrigation, while under drought, P_2 (ICG 4670) and BC_2 (F_1 × ICG 4670) was superior. BC_1 (F_1 × TAG-24) recorded higher shelling percentage and harvest index under irrigation, whereas BC_2 (F_1 × ICG 4670) performed better under drought for the same traits.
Generation mean analysis revealed that the simple additive dominance model was inadequate and thus a six-parameter model was employed. Significant A, B, C and D scaling tests and joint scaling test indicated the presence of higher-order interactions. Under irrigated conditions, dominance (h) and dominance × dominance (l) interactions were significant for days to 50% flowering, days to maturity, number of branches per plant, number of mature pods, haulm yield and dry pod yield, suggesting the prevalence of non-additive gene action. Under drought stress, dominance and dominance × dominance effects were again predominant for dry pod yield, implying that these traits can be improved through hybridization and delayed selection.
Additive (d) and additive × additive (i) gene effects were significant for certain traits including dry pod yield and number of mature pods per plant, indicating that early-generation selection could be effective for these traits. Duplicate epistasis was more common than complementary epistasis under both environments, suggesting mild selection in early generations and more intense selection in advanced generations. The integration of morphological attributes in breeding programmes can significantly enhance screening efficiency and the development of drought-resilient groundnut varieties.

Keywords: Groundnut, drought stress, mean performance, gene action, generation mean analysis

Introduction
Groundnut (*Arachis hypogaea* L.) is an important food and oilseed crop valued for its high oil (47-53%) and protein (25-36%) content. As a self-pollinated tetraploid (2n = 4x = 40) with a geocarpic fruiting habit, it thrives across diverse agro-ecological regions and serves as a major source of edible oil, industrial raw material and nutrient-rich fodder. Its wide adaptability and short duration make it suitable for multiple cropping seasons, thereby supporting crop improvement programmes.
Globally, groundnut is the fifth most cultivated oilseed crop, occupying 27.9 million hectares with an annual production of 47 million tonnes with an average yield of 1676 kg/ha. India ranks second in production, with major contributions from Gujarat, Rajasthan, Madhya Pradesh, Karnataka, Tamil Nadu, Andhra Pradesh and Maharashtra.

Gujarat is leading state in area (169.53 lakh ha) followed by Rajasthan (89.06), during the year 2023-24. (Ministry of Agriculture and Farmers Welfare, Govt. of India). Global groundnut agriculture covers 4.96 million hectares and produces 10.03 million tons with a productivity of 1616 kg/ha (FAOSTAT, 2023) [11]. Despite its significance, productivity remains low because nearly 80% of the crop is grown under rainfed conditions, making it highly vulnerable to erratic and insufficient rainfall. With the demand for vegetable oils projected to double by 2040, enhancing groundnut productivity under water-limited environments has become essential.

Drought is the most critical abiotic stress limiting groundnut yield, compromising flowering, pod formation and kernel filling. Conventional selection for yield under drought is often unreliable due to high genotype × environment interactions. Therefore, understanding the genetic basis of morphological traits associated with drought tolerance is necessary to design efficient breeding strategies. Generation mean analysis enables partitioning of additive, dominance and epistatic gene effects, providing insights into trait inheritance. This study evaluates multiple generations of groundnut to identify key morphological determinants of drought tolerance and the gene actions governing their expression.

Despite the importance of morphological traits in drought tolerance, limited information exists on how these traits are inherited across generations in groundnut. Thus, the present investigation focused solely on morphological observations to elucidate trait expression under irrigated and drought condition and to estimate the nature of gene action governing these traits.

Materials and Methods

The present investigation was conducted at the field of AICRP on summer groundnut, Mahatma Phule Krishi Vidyapeeth, Rahuri, Ahmednagar (MS) during *Kharif*-2023, *Summer*-2024 and *Kharif*-2024. Six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) were developed from cross TAG-24 × ICG 4670 for drought tolerance and pod yield. The experimental material consisted drought tolerant parent as donor and recipient parent is high yielding and wider adaptability of groundnut genotypes. The cross TAG-24 × ICG 4670 was effected in *Kharif*-2023 to produce the F_1 seeds and breeding material like F_1, F_2, BC_1 and BC_2 and advancement was attempted in *Summer*-2024. During *Kharif*-2024, final evaluation trial conducted for study of inheritance of drought tolerance related traits and generation mean analysis, for yield and yield contributing characters under both irrigated and drought (rainout shelter) condition The characters *viz.*, days to 50 percent flowering, days to maturity, number of branches per plant, number of mature pods per plant, haulm yield per plant, dry pod yield per plant, hundred kernel weight, shelling percentage and harvest index on dry weight basis were analysed for this study.

Each character was analysed separately and the ANOVA was constructed as per Panse and Sukhatme (1995) [26]. The data was analyzed for mean performance of the generations. Gene action has been worked by generation mean analysis as per six parameter model given by (Hayman, 1958) [14]. Adequacy of additive dominance effect was detected by individual scaling test, three tests of scale were carried out to detect presence or absence of gene interaction by using formulae given by Mather (1949) [20] and Hayman and Mather (1957) [15]. Cavalli's (1952) Joint scaling test was applied to test the adequacy of additive-dominance model. Whenever, the model was found inadequate, Hayman (1958) [14] six parameter model was used to estimate the different gene effects. Statistical analysis of data was done by using software package INDOSTAT.

Results and Discussion

Analysis of Variances

The analysis of variance for nine characters is presented in Table 1 for two crosses under both irrigated and drought (rainout shelter) condition.

Under irrigated condition (Table 1), the analysis of variance revealed significant differences among treatments in cross TAG-24 × ICG 4670 i.e., parents and their derived generations (F_1, F_2, BC_1 and BC_2) for all traits studied. This indicates the presence of substantial genetic variability among the parents and their progenies.

Under drought condition (Table 1), the analysis of variance showed significant differences among treatments in cross TAG-24 × ICG 4670 i.e., parents and their respective generations (F_1, F_2, BC_1 and BC_2) for the majority of traits, indicating considerable genetic variability under moisture stress. However, trait such as haulm yield exhibited non-significant differences, suggesting limited genetic variation for this character.

Mean performance of parents and generations

The mean performance of parents and their crosses for pod yield per plant and its contributing traits in groundnut are presented in Table 2.1 and 2.2 for irrigated and drought condition respectively. Higher values are desirable for all traits under study except for days to flowering, days to maturity for which lower values are preferred. The trait wise results are discussed as below:

Cross: TAG-24 × ICG 4670

Days to 50% flowering

Under irrigated condition, the mean values for days to 50% flowering across parents and generations ranged between 35.86 and 45.33 days. Among the parental genotypes, ICG 4670 exhibited the earliest flowering (35.86 days), whereas TAG-24 showed the latest (45.33 days). Among the derived generations, BC_2 recorded the earliest flowering (37.26 days), followed by F_1 (40.53 days), BC_1 (41.56 days) and F_2 (42.80 days). This trend suggests that backcross generations, particularly BC_2, may contribute to the development of early flowering lines under irrigated conditions, which could be beneficial for fitting into shorter cropping durations.

Under drought stress, the mean values for days to 50% flowering among the parental and hybrid generations ranged from 33.80 to 41.33 days. Among the parents, ICG 4670 exhibited the earliest flowering (33.80 days), whereas TAG-24 recorded the latest (41.33 days). Among the derived generations, the BC_2 population showed the earliest flowering (36.16 days), followed by F_1 (36.46 days) and BC_1 (38.53 days). The F_2 generation exhibited the most delayed flowering (39.38 days). These findings suggest that certain backcross generations, particularly BC_2, may possess drought escape mechanisms through earlier flowering, which is a critical adaptive trait under water-limited environments.

Days to Maturity

Under irrigated condition, the mean values for days to maturity among the parents and derived generations varied from 102.67 to 112.30 days. The BC_1 generation recorded the earliest maturity (104.26 days), followed by F_1 (107.60 days), BC_1 (107.73 days) and F_2 (112.30 days). Among the parental lines, ICG 4670 matured earlier (102.67 days), while TAG-24 required the longest duration to reach maturity (111.66 days). These results suggest that the F_1 and backcross generations have inherited early maturity traits from the early-maturing parent, ICG 4670, which can be advantageous for escaping terminal stress in water-limited or late-sown conditions.

Under drought stress, the days to maturity among the parental and hybrid generations ranged from 97.66 to 106.00 days. The BC_2 generation matured the earliest (100.18 days), followed by F_2 (102.18 days), F_1 (102.20 days) and BC_1 (104.20 days). Among the parents, ICG 4670 matured earlier (97.66 days), while TAG-24 again required a longer duration (106.00 days). Compared to irrigated conditions, a slight advancement in maturity was observed across most generations, indicating a stress-induced acceleration of phenological development. This early maturity under stress, particularly in F_1 and BC_2, may serve as an important drought-escape strategy.

Number of branches/plant

Under irrigated condition, the number of branches per plant varied from 4.86 to 7.40 across the parents and their derived generations. The highest number of branches was recorded in the BC_1 generation (6.31), followed by F_2 (6.24), F_1 (5.40) and BC_2 (4.68). Among the parents, TAG-24 exhibited a higher branching habit (7.40), while ICG 4670 recorded the lowest (4.86). The increased number of branches in BC_1 and F_2 generations under optimum water availability indicates the presence of heterosis and favorable genetic recombination contributing to enhanced vegetative growth.

Under drought stress, the number of branches per plant declined across all generations, ranging from 4.96 to 6.04. The F_2 generation recorded the highest number of branches (6.04), followed by F_1 (5.13), BC_2 (5.10) and BC_1 (4.96). Among the parents, ICG 4670 maintained a higher branching ability (5.86), while TAG-24 exhibited the lowest value (5.53). The reduction in branch number under drought conditions indicates the negative impact of water deficit on vegetative growth. However, the relatively higher number of branches maintained by the F_2 and F_1 generations suggests a better adaptability and potential to sustain vegetative vigor under stress environments.

Number of mature pods/plant

Under irrigated condition, the number of mature pods per plant varied widely among generations, ranging from 14.33 to 20.40. The BC_1 generation recorded the highest number of mature pods (18.10), followed closely by F_2 (17.95), F_1 (17.06) and BC_2 (14.58). Among the parents, TAG-24 exhibited a better pod set (20.40), while ICG 4670 had a comparatively lower pod number (14.33). The higher pod numbers observed in BC_1 and F_2 suggest heterotic advantage and transgressive segregation, indicating that the hybrids inherited and combined favorable alleles for reproductive efficiency from both parents.

Under drought stress, the number of mature pods per plant was considerably reduced across parent first related generations. While, P_2 related generations show considerable improvement in pod set. It was ranging from 16.20 to 19.73. Despite the stress conditions, the BC_2 generation recorded the highest pod number (18.50), followed by F_2 (18.35), F_1 (17.33) and BC_1 (17.18). Among the parents, ICG 4670 produced more pods (19.73) than TAG-24 (16.20). The relatively higher pod production in BC_2 and F_2 indicates better reproductive resilience and potential drought adaptability. This trait is critical for yield stability under stress conditions.

Haulm yield/plant (g)

Under irrigated condition, haulms yield per plant ranged from (18.59 g) to (29.54 g) across parents and generations. The highest haulm yield was observed in the F_2 generation (26.30 g), followed by F_1 (25.60 g), BC_1 (23.74 g) and BC_2 (20.39 g). Among the parental lines, TAG-24 recorded a higher haulm yield (29.54 g) as compared to ICG 4670 (18.59 g). The significantly higher biomass accumulation in F_2 and F_1 suggests the influence of heterosis. This increased vegetative biomass is indicative of better growth and nutrient assimilation, which can indirectly support improved reproductive performance as well.

Under drought condition, haulms yield per plant exhibited a noticeable reduction in first parent i.e. TAG-24 (21.56 g) and simultaneously increase in second parent i.e. ICG 4670 (23.45 g). The mean was ranging from (21.56 g) to (23.45 g) across parents and generations. The BC_2 generation maintained the highest haulm yield (22.74 g) followed by BC_1 (22.63 g), F_2 (22.20 g) and F_1 (21.86 g). Among the parents, ICG 4670 recorded a higher haulm biomass (23.45 g) compared to TAG-24 (21.56 g). The overall decline in biomass under water-limited conditions highlights the adverse effect of drought on vegetative growth. However, the ability of P_2 and BC_2 to retain relatively higher haulm yields under stress signifies better physiological resilience and suggests their utility in drought tolerant breeding programs.

Dry pod yield/plant (g)

Under irrigated condition, the dry pod yield per plant exhibited substantial variation among different generations, ranging from 15.52 g to 19.87 g. The F_2 generation recorded the maximum yield (19.87 g), followed by F_1 (18.08 g), BC_1 (17.64 g) and BC_2 (15.52 g). Among the parental lines, TAG-24 produced a higher pod yield (19.27 g), whereas ICG 4670 recorded a lower yield (15.58 g). These results suggest that the F_2 and F_1 generations possess enhanced yield potential, likely due to hybrid vigor and favorable genetic combinations. High pod yield under optimal water availability reflects improved partitioning of assimilates towards reproductive structures, making these generations promising candidates for further evaluation.

Under drought stress, a noticeable decline in dry pod yield per plant was observed across all generations except P_2 and BC_2, with values ranging from 16.51 g to 19.67 g. Among the generations, BC_2 recorded the highest pod yield (18.26 g), followed by F_1 (17.85 g), F_2 (17.54 g) and BC_1 (16.80 g). In comparison, the parental line TAG-24 yielded (16.51 g), whereas ICG 4670 showed the highest yield (19.67 g). The reduction in pod yield except P_2 and BC_2 under water-deficit conditions underscores the negative impact of drought on reproductive output. Nonetheless, the BC_2 and F_1 generations maintained relatively higher yield which indicating their superior adaptability and potential for use in drought resilient breeding programs.

100 kernel weight (g)

Under irrigated condition, the 100-kernel weight among parents and generations ranged from (24.86 g) to (32.84 g). The highest kernel weight was observed in the BC_1 generation (32.65 g), followed by F_1 (30.02 g), F_2 (28.38 g) and BC_2 (26.05 g). Among the parents, TAG-24 recorded a higher kernel weight (32.84 g) as compared to ICG 4670 (24.86 g). The relatively greater seed mass in BC_1 and F_1 may be attributed to hybrid vigour and enhanced translocation of assimilates towards seed development under optimal moisture.

Under drought stress, the 100 kernel weight exhibited a significant reduction compared to irrigated conditions except P_2 and BC_2, with values ranging from (23.80 g) to (27.43 g). The BC_2 generation maintained the highest kernel weight (26.80 g), followed by F_1 (24.95 g), F_2 (24.69 g) and BC_1 (23.80 g). Among the parents, TAG-24 recorded (24.54 g), while ICG 4670 showed the highest value (27.43 g).

Shelling percentage (%)

Under irrigated condition, the shelling percentage varied from (64.23%) to (71.98%) across the parental lines and their derived generations. The BC_1 generation exhibited the highest shelling percentage (69.50%), followed by F_1 (68.11%), F_2 (66.75%) and BC_2 (64.55%). Among the parents, TAG-24 recorded a shelling percentage of (71.98%), while ICG 4670 showed a lower value of (64.23%). The superior shelling performance of the BC_1 and F_1 generations under optimal moisture suggests efficient kernel filling and improved seed to pod ratio. High shelling percentage under irrigated conditions is a desirable trait for enhancing marketable yield and improving economic returns.

Under drought conditions, a slight reduction in shelling percentage was observed across all generations except P_2 and BC_2, with values ranging from (63.50%) to (66.37%). The BC_2 generation maintained the highest shelling percentage (64.86%), followed by F_2 (64.68%), BC_1 (63.75%) and F_1 (63.61%). Among the parents, TAG-24 recorded 63.50%, whereas ICG 4670 registered the highest (66.37%). Although drought stress led to marginal declines in shelling efficiency, the BC_2 and F_2 generations retained relatively higher values, suggesting their resilience in maintaining seed recovery.

Harvest index (%)

Under irrigated condition, the harvest index ranged from (37.11%) to (41.85%) among the parental lines and their generations. The highest value was recorded in the BC_1 generation (38.59%) followed by F_1 (38.50%), F_2 (37.48%) and BC_2 (36.71%). Among the parents, TAG-24 had a harvest index of (41.85%), while ICG 4670 recorded the lowest (37.11%). The superior performance of BC_1 and F_1 indicates efficient translocation of assimilates towards the reproductive sink under optimal water availability. A higher harvest index under irrigation reflects better resource use efficiency and is an important trait for improving overall productivity.

Under drought stress, the harvest index exhibited a noticeable decline across all generations except P_2 and BC_2, ranging from (34.33%) to (38.81%). The BC_2 generation showed the highest value (37.51%), followed by F_2 (37.41%), F_1 (36.02%) and BC_1 (34.86%). Among the parents, TAG-24 and ICG 4670 recorded harvest index of 34.33% and 38.81% respectively. Although overall values were lower than under irrigated conditions, BC_2 and F_2 generations maintained relatively higher values reflecting their efficiency in biomass partitioning under moisture limited environments. A stable harvest index under drought is indicative of genotypes with better stress resilience and yield potential.

Estimates of scaling tests for detecting non-allelic interactions

The results on scaling test (A, B, C and D) in respect of yield, yield contributing and drought tolerance related traits have been tabulated in (Table 3) under irrigated and drought stress (rainout shelter) condition. The result for cross: TAG-24 × ICG 4670 is mentioned under two conditions as follow:

Under irrigated condition (Table 3)

Days to 50% flowering

For the days to 50% flowering, the scaling test 'D' (6.76) was positively significant in cross TAG-24 × ICG 4670. Joint scaling test was found highly significant, indicating the presence of epistasis.

Days to maturity

In case of days to maturity, scaling tests 'D' (12.61) was positively significant in cross TAG-24 × ICG 4670. The joint scaling test was found highly significant for days to maturity in cross TAG-24 × ICG 4670, indicating inadequacy of additive dominance model to explain all the genetic variation.

Number of mature pods/plant

Scaling test 'B' (-2.23) was negatively significant. While, scaling test 'D' (3.23) for cross TAG-24 × ICG 4670 was positively significant. Estimates of genetic effects for this trait by joint scaling test indicated inadequacy of additive dominance model to explain all the genetic variations as the chi-square values of all the crosses were significant.

Haulm yield/plant

For haulm yield per plant, scaling tests 'C' (9.89) and 'D' (6.47) were significant, showing additive dominance model was inadequate to explain all the genetic variations.

Dry pod yield/plant

In case of dry pod yield per plant, scaling tests 'C' (10.46) and 'D' (6.58) were positively significant. Estimates of genetic effects for this trait by joint scaling test indicated inadequacy of additive dominance model to explain all the genetic variations as the chi-square values of both the crosses were significant.

100 kernel weight

For 100 kernel weight, no scaling tests were found significant in cross TAG-24 × ICG 4670. All joint scaling tests were found non-significant, indicating adequacy of additive dominance model to explain all the genetic variation.

Shelling percentage
In case of shelling percentage, all joint scaling tests were found non-significant showing additive dominance model was inadequate to explain all the genetic variations.

Harvest index
All scaling test 'A', 'B', 'C' and 'D' were non-significant, showing adequacy of additive dominance model to explain all the genetic variation as the chi-square values of both the crosses were non-significant.

Under drought condition (Table 3)
Days to 50% flowering
For Days to 50% flowering, scaling tests 'C' (9.46) and 'D' (4.06) were positively significant, showing additive dominance model was inadequate to explain all the genetic variations.

Days to maturity
All scaling test 'A', 'B', 'C' and 'D' were non-significant which shows adequacy of additive dominance model to explain all the genetic variation as the chi-square values of both the crosses were non-significant.

Number of mature pods/plant
Scaling tests tests 'C' (2.50) and 'D' (2.01) were positively significant, showing additive dominance model was inadequate to explain all the genetic variations as the chi-square values of both the crosses were significant.

Haulm yield/plant
All scaling tests 'A', 'B', 'C' and 'D' were non-significant which shows adequacy of additive dominance model to explain all the genetic variation as the chi-square values of both the crosses were non-significant.

Dry pod yield/plant
In case of dry pod yield per plant, scaling tests 'A' (0.43) and 'B' (0.21) were positively significant. Estimates of genetic effects for this trait by joint scaling test indicated inadequacy of additive dominance model to explain all the genetic variations as the chi-square values of both the crosses were significant.

100 kernel weight
All scaling tests 'A', 'B', 'C' and 'D' were non-significant which shows adequacy of additive dominance model to explain all the genetic variation as the chi-square values of both the crosses were non-significant.

Shelling percentage
All scaling tests 'A', 'B', 'C' and 'D' were non-significant which shows adequacy of additive dominance model to explain all the genetic variation as the chi-square values of both the crosses were non-significant.

Harvest index
For harvest index, no scaling tests were found significant, indicating adequacy of additive dominance model to explain all the genetic variation.

Estimates of gene effects for yield and yield contributing characters
The estimates of m (mean), major genetic effects additive [d] and dominance [h] and non-allelic gene interactions (i, j and l) based on six parameter model (Hayman, 1958) [14] for pod yield, yield contributing traits for cross: TAG-24 × ICG 4670 (Table 4 and Table 5) under both irrigated and drought stress condition respectively. The parameter [m] was significant for all the characters under study.

Cross: TAG-24 × ICG 4670
The gene effects estimated by using perfect fit model in respect of traits associated with pod yield in groundnut has been presented in Table 4 and Table 5 for irrigated and drought condition respectively.

Days to 50% flowering
Under irrigated condition, the estimates of genetic parameters, it was observed that 'd' (4.30) was positively significant while 'h' (-13.60) was negatively significant. The interaction components 'l' (18.13) was estimated positively significant. Opposite sign observed for genetic component dominance 'h' and dominance x dominance 'l', with presence of duplicate epistasis.
Under drought stress, from estimates of genetic parameters, it was observed that 'd' (2.36) was positively significant while 'h' (-9.23) was negatively significant. The interaction component 'i' (-8.13) was observed negatively significant, while 'l' (6.80) was estimated positively significant. Opposite sign observed for genetic component dominance 'h' and dominance x dominance 'l', with presence of duplicate epistasis. The presence of additive, dominance and epistatic interactions for this trait were earlier reported by Kalaimani and Thangavelu (1996) [17], Jayalakshmi and Reddy (2002) [16], Suneetha *et al.*, (2006) [36] and Boraiah *et al.*, (2015) [6]. While, Parameshwarappa and Kumar (2007) [27] reported dominance x dominance genetic effects for days to flowering.

Days to maturity
Under irrigated condition, from the estimates of genetic parameters, it was observed that 'h' (-24.80) was negatively significant. The interaction components, 'i' (-25.23) was observed negatively significant, while 'l' (30.76) was estimated positively significant. Opposite sign observed for genetic component dominance 'h' and dominance x dominance 'l', revealing epistasis was predominantly of duplicate type.
Under drought stress, from estimates of genetic parameters, it was observed that significant mean (m) effects were observed, but additive (d) and dominance (h) effects were non-significant, indicating an absence of non-allelic interactions for this trait. Role of additive and non-additive gene action for days to maturity were earlier reported by, Talwar *et al.*, (1983) [37] in soybean crop while in groundnut by Basu *et al.*, (1988) [5], Suneetha *et al.*, (2006) [36], Gaurav *et al.*, (2010) [12] Pavithradevi (2013) [29], Prabhu *et al.*, (2016) [30] and Shinde *et al.*, (2016) [34].

Number of branches/plant
Under irrigated condition, from estimates of genetic parameters, it was observed that 'd' (1.63) was positively significant while 'h' (-3.70) was negatively significant. The interaction component 'i' (-2.96) was observed negatively significant, however 'l' (4.03) was estimated positively significant. Opposite sign observed for genetic component dominance 'h' and dominance x dominance 'l', with

presence of duplicate epistasis.

Under drought stress, from estimates of genetics parameters, it was observed that ‘h’ (-4.60) was negatively significant. The interaction component ‘i’ (-4.03) was observed negatively significant, while ‘l’ (5.56) was estimated positively significant. Opposite sign observed for genetic component dominance ‘h’ and dominance x dominance ‘l’, revealing epistasis was predominantly of duplicate type. The duplicate type of epistasis was earlier noticed by Rahangdale and Raut (2002) [31], Amrita *et al.*, (2014) [2] and Nagarajan *et al.*, (2022) [24].

Number of mature pods/plant

Under irrigated condition, from estimates of genetic parameters, it was observed that ‘d’ (3.51) was positively significant while ‘h’ (-6.76) was negatively significant. The interaction component ‘i’ (-6.46) was observed negatively significant, however ‘l’ (9.96) was estimated positively significant. Opposite sign observed for genetic component dominance ‘h’ and dominance x dominance ‘l’, with presence of duplicate epistasis.

Under drought condition, significant mean (m) effects with high magnitude were observed. Additive (d) (-1.76) effect was negatively significant, but non-allelic interactions were absent, suggesting the preponderance of dominant gene effects for number of mature pods per plant. It revealed their potential in controlling this character in this cross which supports the earlier findings of Kaw and Menon (1983) [18], Cecon *et al.*, (1985) [8] and Nagabushanam *et al.*, (1992) in groundnut, also, similar results were reported by Rahangdale and Raut (2002) [31] and Nagarajan *et al.*, (2022) [24].

Haulm yield/plant (g)

Under irrigated condition, the estimates of genetic parameters, it was observed that ‘d’ (5.34) was positively significant while ‘h’ (-13.42) was negatively significant. The interaction components ‘l’ (16.01) was estimated positively significant. Opposite sign observed for genetic component dominance ‘h’ and dominance x dominance ‘l’, with presence of duplicate epistasis.

Under drought stress, from estimates of genetic parameters, it was observed that significant mean (m) effects were observed, but additive (d) and dominance (h) effects were non-significant, indicating an absence of non-allelic interactions for this trait. This was in conformity with previous findings such as Nigam S. N. (2014) observed both additive and non-additive gene effects; while, Patil *et al.*, (2017) observed non-additive gene effects.

Dry pod yield/plant (g)

Under irrigated condition, from estimates of genetic parameters, it was observed that ‘d’ (2.11) was positively significant while ‘h’ (-13.50) was negatively significant. The interaction component ‘i’ (-13.16) was observed negatively significant, however ‘l’ (15.86) was estimated positively significant. Opposite sign observed for genetic component dominance ‘h’ and dominance x dominance ‘l’, with presence of duplicate epistasis.

Under drought stress, from estimates of genetic parameters, it was observed that ‘d’ (-1.46) and ‘h’ (-2.27) were negatively significant. The interaction component ‘l’ (0.18) was estimated positively significant. Opposite sign observed for genetic component dominance ‘h’ and dominance x dominance ‘l’, revealing epistasis was predominantly of duplicate type. Gaurav *et al.*, (2010) [12], Shoba *et al.*, (2010) [35] and Nagarajan *et al.*, (2022) [24] reported additive gene action to be involved in the inheritance of this trait. However, non-additive gene action holds good for this trait were reported by Mothilal and Ezhil (2010) [22], Savithramma *et al.*, (2010) [32], Pavithradevi (2013) [29] and Azad *et al.*, (2014) [4]. Although, importance of both additive and non-additive gene action in the inheritance of this trait was observed by Makne and Bhale (1989) [19] in groundnut.

100 kernel weight (g)

Under irrigated condition, significant mean (m) (26.14) effect with high magnitude were observed. Additive (d) (5.15) effect was positively significant, but non-allelic interactions were absent, suggesting the preponderance of additive gene effects for 100 kernel weight.

Under drought condition, significant mean (m) (23.54) effects with high magnitude were observed. Additive (d) (-1.44) effect was negatively significant, but non-allelic interactions were absent, suggesting the preponderance of dominant gene effects for 100 kernel weight. Role of additive and non-additive gene action for 100-kernel weight were earlier reported by Senthil and Varman (1998) [33], Gaurav *et al.*, (2010) [12], Pavithradevi (2013) [29] and Prabhu *et al.*, (2016) [30] respectively. Interestingly, Hariprasanna *et al.*, (2008) [13] reported predominance of additive gene action in the expression of 100-seed weight.

Shelling percentage (%)

Under irrigated condition, significant mean (m) (66.99) effect with high magnitude were observed. Additive (d) (3.87) effect was positively significant, but non-allelic interactions were absent, suggesting the preponderance of additive gene effects for shelling percentage.

Under drought stress, from estimates of genetic parameters, it was observed that significant mean (m) (66.41) effect was observed, but additive (d) and dominance (h) effects were non-significant, indicating an absence of non-allelic interactions for this trait. This was confirmed with earlier findings, Dobaria *et al.*, (2003) [10] observed both additive and dominant genetic effects in case of shelling out-tum. However, Adamu *et al.*, (2008) [1] reported major role of non-additive gene action as well as dominance x dominance genetic interaction for shelling percent.

Harvest index (%)

Under irrigated condition, significant mean (m) (38.80) effect with high magnitude were observed. Additive (d) (2.36) effect was positively significant, but non-allelic interactions were absent, suggesting the preponderance of additive gene effects for harvest index.

Under drought condition, significant mean (m) (41.48) effects with high magnitude were observed. Additive (d) (-2.23) effect was negatively significant, but non-allelic interactions were absent, suggesting the preponderance of dominant gene effects for harvest index. Previously, the additive gene effect for harvest index trait is supported by Chavadhari *et al.*, (2017) [9]. Nonetheless, Apparao (2000) [3] reported predominant non-additive genetic effects governing this trait.

Table 1: Analysis of variance (ANOVA) of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for pod yield and yield contributing traits for Cross: TAG-24 × ICG 4670 of groundnut under irrigated and drought condition.

Sr. No.	Name of characters	Cross: TAG-24 × ICG 4670			
		Irrigated Condition		Drought Condition	
		Mean sum of squares		Mean sum of squares	
		Generations	Generations	Generations	Error
	Degree of Freedom	5	5	5	10
1.	Days to 50% flowering (DFF)	37.10**	20.53**	20.53**	1.51
2.	Days to maturity (DM)	44.33**	25.60**	25.60**	1.25
3.	Number of branches/plants (NBPP)	3.18**	0.49*	0.49*	0.63
4.	Number of mature pods/plants (NMPP)	16.29**	4.59**	4.59**	1.26
5.	Haulm yield (g/plant) (HYP)	48.83**	0.80	0.80	0.90
6.	Dry pod yield (g/plant) (DrYPP)	9.83**	3.86**	3.86**	14.63
7.	100 kernel weight (g/plant)	46.18**	6.02**	6.02**	0.66
8.	Shelling Percentage (%)	26.62**	3.60**	3.60**	0.93
9.	Harvest index (HI)	10.35*	8.87**	8.87**	1.53
Note: *, ** significant at P = 0.05 and 0.01 percent levels, respectively.					

Table 2.1: Mean performance of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for yield and yield contributing traits under irrigated condition in Cross: TAG-24 × ICG 4670

Generations	P_1	P_2	F_1	F_2	BC_1	BC_2
Days to 50% flowering (DFF)	45.33 ± 1.71	35.86 ± 1.40	40.53 ± 1.55	42.80 ± 0.72	41.56 ± 0.73	37.26 ± 0.68
Days to maturity (DM)	111.66 ± 4.28	102.67 ± 3.91	107.60 ± 4.13	112.30 ± 1.83	107.73 ± 1.86	104.26 ± 1.85
Number of branches/plants (NBPP)	7.40 ± 0.34	4.86 ± 0.27	5.40 ± 0.28	6.24 ± 0.13	6.31 ± 0.15	4.68 ± 0.10
Number of mature pods/plants (NMPP)	20.40 ± 0.81	14.33 ± 0.59	17.06 ± 0.70	17.95 ± 0.30	18.10 ± 0.33	14.58 ± 0.28
Haulm yield (g/plant) (HYP)	29.54 ± 1.14	18.59 ± 0.73	25.60 ± 0.92	26.30 ± 0.44	23.74 ± 0.45	20.39 ± 0.37
Dry pod yield (g/plant) (DrYPP)	19.27 ± 0.75	15.58 ± 0.64	18.08 ± 0.67	19.87 ± 0.34	17.64 ± 0.32	15.52 ± 0.29
100 kernel weight (g/plant)	32.84 ± 1.37	24.86 ± 1.01	30.02 ± 1.19	28.38 ± 0.46	32.65 ± 0.57	26.05 ± 0.48
Shelling Percentage (%)	71.98 ± 2.76	64.23 ± 2.46	68.11 ± 2.61	66.75 ± 1.09	69.50 ± 1.20	64.55 ± 1.15
Harvest index (HI)	41.85 ± 1.64	37.11 ± 1.44	38.50 ± 1.49	37.48 ± 0.62	38.59 ± 0.67	36.71 ± 0.66

Table 2.2: Mean performance of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for yield and yield contributing traits under drought condition in Cross: TAG-24 × ICG 4670

Generations	P_1	P_2	F_1	F_2	BC_1	BC_2
Days to 50% flowering (DFF)	41.33 ± 1.62	33.80 ± 1.32	36.46 ± 1.40	39.38 ± 0.65	38.53 ± 0.69	36.16 ± 0.64
Days to maturity (DM)	106.00 ± 4.04	97.66 ± 3.75	102.20 ± 3.91	102.18 ± 1.68	104.20 ± 1.78	100.18 ± 1.76
Number of branches/plants (NBPP)	5.53 ± 0.30	5.86 ± 0.27	5.13 ± 0.23	6.04 ± 0.12	4.96 ± 0.11	5.10 ± 0.13
Number of mature pods/plants (NMPP)	16.20 ± 0.63	19.73 ± 0.85	17.33 ± 0.70	18.35 ± 0.33	17.18 ± 0.30	18.50 ± 0.35
Haulm yield (g/plant) (HYP)	21.56 ± 0.93	23.45 ± 0.92	21.86 ± 1.04	22.20 ± 0.38	22.63 ± 0.40	22.74 ± 0.41
Dry pod yield (g/plant) (DrYPP)	16.51 ± 0.66	19.67 ± 0.76	17.85 ± 0.67	17.54 ± 0.29	16.80 ± 0.30	18.26 ± 0.33
100 kernel weight (g/plant)	24.54 ± 0.94	27.43 ± 1.08	24.95 ± 1.00	24.69 ± 0.41	23.80 ± 0.42	26.80 ± 0.48
Shelling Percentage (%)	63.50 ± 2.44	66.37 ± 2.54	63.61 ± 2.43	64.68 ± 1.06	63.75 ± 1.10	64.86 ± 1.15
Harvest index (HI)	34.33 ± 1.33	38.81 ± 1.51	36.02 ± 1.40	37.41 ± 0.62	34.86 ± 0.60	37.51 ± 0.68

Table 3: Estimation of scaling test and Chi square ($\chi 2$) test for yield and yield contributing traits under irrigated and drought condition in Cross: TAG-24 × ICG 4670of groundnut

Characters	Cross: TAG-24 × ICG 4670									
	Irrigated condition					Drought Condition				
	A	B	C	D	χ^2	A	B	C	D	χ^2
Days to 50% flowering	-2.73	-1.86	8.93	6.76**	14.68**	-0.73	2.06	9.46*	4.06**	8.65**
Days to maturity	-3.80	-1.73	19.70	12.61**	7.98*	0.20	0.50	0.66	-0.02	0.017
Number of branches/plants	-0.16	-0.90*	1.90*	1.48**	24.59**	-0.73	-0.80	2.50**	2.01**	51.55**
Number of mature pods/plants	-1.26	-2.23*	2.96	3.23**	20.52**	0.83	-0.06	2.83	1.03	2.84
Haulm yield	-1.65	-1.40	9.89**	6.47**	36.91**	0.44	0.76	-0.72	-0.96	4.70
Dry pod yield	-1.07	-1.62	10.46**	6.58**	68.06**	0.43*	0.21*	1.48	0.41	3.24*
100 kernel weight	0.12	-2.78	-6.53	-1.93	6.75	-1.88	1.21	-3.10	-1.22	5.71
Shelling Percentage	-1.07	-3.22	-5.41	-0.55	0.78	0.40	-0.24	1.63	0.74	1.41
Harvest index	-3.15	-2.18	-6.01	-0.33	2.95	-0.63	0.19	4.47	2.45	2.85

Note: *, ** significant at P = 0.05 and 0.01 percent levels, respectively.

Table 4: Estimation of gene effect for yield and yield contributing traits under irrigated condition in Cross: TAG-24 × ICG 4670

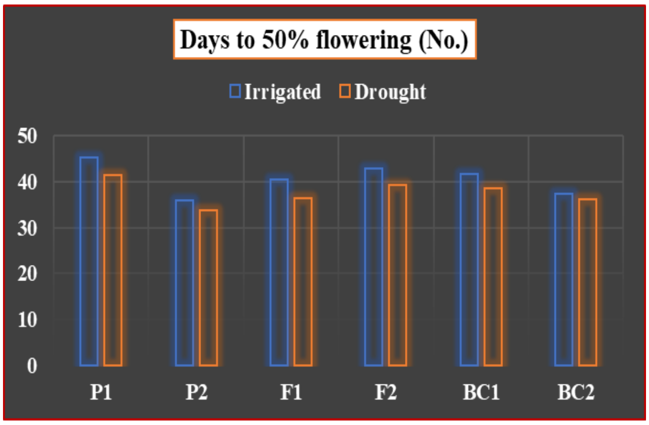
Characters	Genetic Parameters						Type of epistasis
	m	d	h	i	j	l	
Days to 50% flowering (DFF)	42.80**	4.30**	-13.60**	-13.53	-0.43	18.13**	Duplicate
Days to maturity (DM)	112.30**	3.46	-24.80**	-25.23**	-1.03	30.76*	Duplicate
Number of branches/plants (NBPP)	6.24**	1.63**	-3.70**	-2.96**	0.36	4.03**	Duplicate
Number of mature pods/plants (NMPP)	17.95**	3.51**	-6.76**	-6.46**	0.48	9.96**	Duplicate
Haulm yield (g/plant) (HYP)	26.31**	5.34**	-13.42**	-12.95	-0.12	16.01**	Duplicate
Dry pod yield (g/plant) (DrYPP)	19.87**	2.11**	-13.50**	-13.16**	0.27	15.86**	Duplicate
100 kernel weight (g/plant)	26.14**	5.15**	5.09	--	--	--	--
Shelling Percentage (%)	66.99**	3.87*	-2.06	--	--	--	--
Harvest index (HI)	38.80**	2.36*	-4.97	--	--	--	--

Note: *, ** significant at P = 0.05 and 0.01 percent levels, respectively.

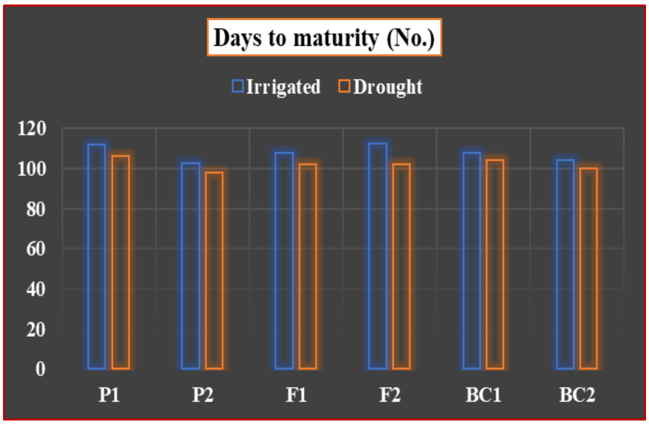
Table 5: Estimation of gene effect for yield and yield contributing traits under drought condition in Cross: TAG-24 × ICG 4670

Characters	Genetic Parameters						Type of epistasis
	m	d	h	i	j	l	
Days to 50% flowering (DFF)	39.38**	2.36**	-9.23**	-8.13**	-1.40	6.80*	Duplicate
Days to maturity (DM)	101.80**	4.16	1.33	--	--	--	--
Number of branches/plants (NBPP)	6.04**	-0.13	-4.60**	-4.03**	0.03	5.56**	Duplicate
Number of mature pods/plants (NMPP)	20.05**	-1.76**	-4.00	--	--	--	--
Haulm yield (g/plant) (HYP)	21.57**	0.05	2.83	--	--	--	--
Dry pod yield (g/plant) (DrYPP)	17.74**	-1.46**	-2.27*	-0.83	0.11	0.18*	Duplicate
100 kernel weight (g/plant)	23.54**	-1.44*	3.18	--	--	--	--
Shelling Percentage (%)	66.41**	-1.43	-4.13	--	--	--	--
Harvest index (HI)	41.48**	-2.23*	-10.82	--	--	--	--

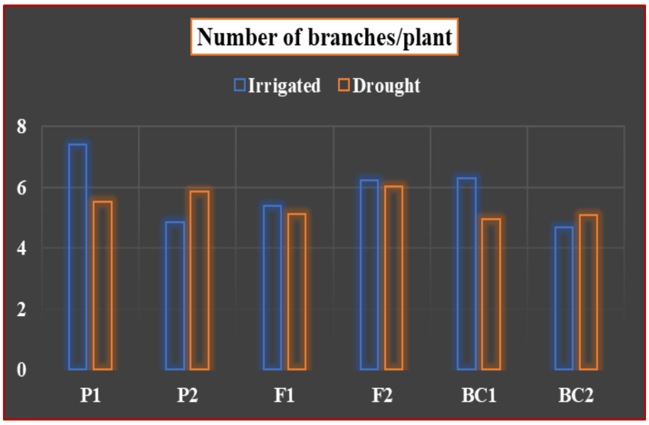
Note: *, ** significant at P = 0.05 and 0.01 percent levels, respectively.



a) Days to 50% flowering

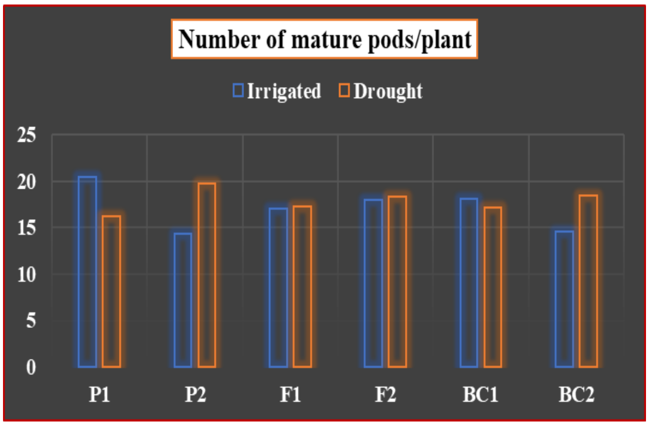


b) Days to maturity

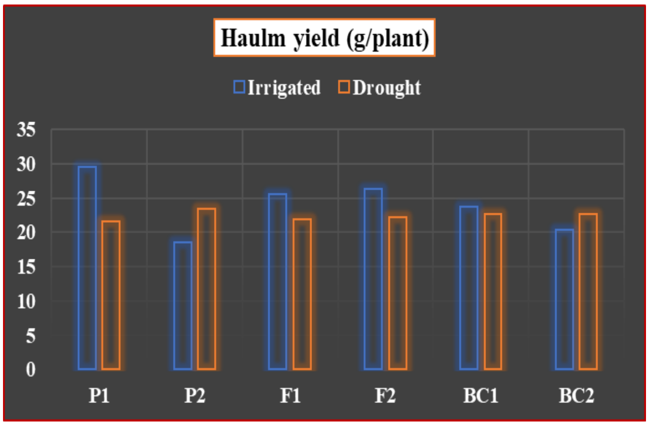


c) Number of branches/plant

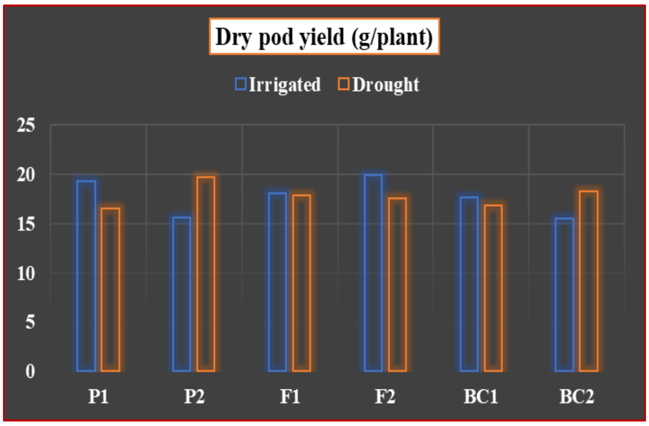
Fig. 1: Comparison of morphological traits across generations under both irrigated and drought conditions



a) Number of mature pods/plant

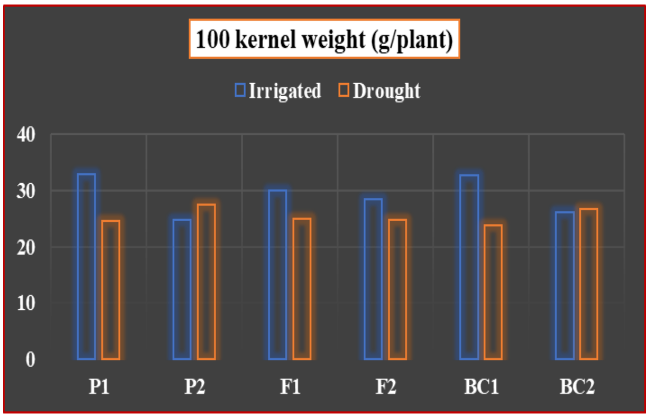


b) Haulm yield

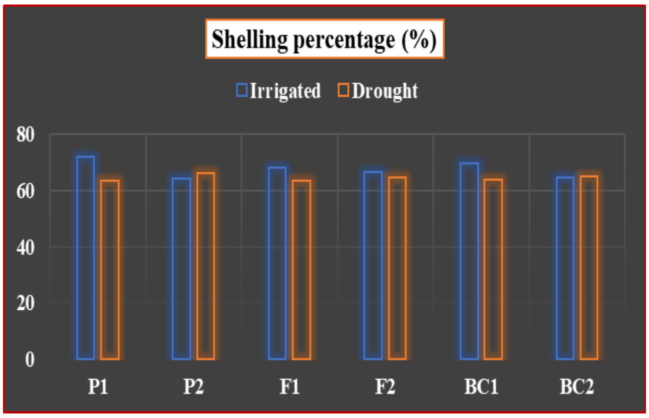


c) Dry pod yield

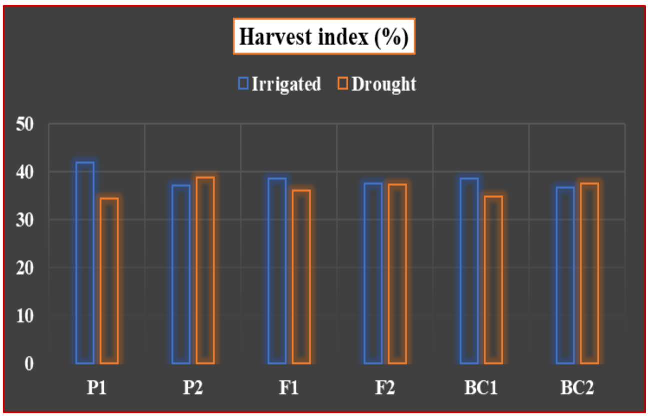
Fig 2: Comparison of morphological traits across generations under both irrigated and drought conditions



a) 100 kernel weight



b) Shelling percentage



c) Harvest index

Fig. 3: Comparison of morphological traits across generations under both irrigated and drought conditions

Conclusion

In nutshell, in the present investigation, it can be inferred that morphological traits showed substantial variability under irrigated and drought stress condition and exhibited distinct inheritance patterns. Dry pod yield and number of mature pods per plant were primarily controlled by additive and additive × additive gene effects, indicating the effectiveness of early-generation selection. In contrast, days to 50% flowering, days to maturity, number of branches per plant, number of mature pods, haulm yield and dry pod yield were governed largely by dominance and dominance × dominance interactions, suggesting that selection and breeding procedures should be modified to exploit this type of non-additive genetic variance by delaying the selection to later generations. Overall, integrating morphological traits with physiological and yield-based indicators can greatly strengthen drought screening and accelerate breeding progress towards developing drought-resilient groundnut cultivars.

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