Direct Research Journal of Agriculture and Food Science

Vol. 12(3), Pp. 73-93, November 2024,

https://journals.directresearchpublisher.org/index.php/drjafs

Research Article
ISSN: 2354-4147

Determining the type of gene action(s) involved in the genetic control of drought-tolerance and yield-associated traits of groundnut (*Arachis hypogaea* L.) using generation mean and variance analysis of parental, F1 and the segregating populations (backcrosses and F2)

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ABSTRACT

In Northern Ghana, groundnut production is severely impacted by drought stress. To create better cultivars, it is essential to understand the genetic processes determining drought tolerance. The objective of this study was to use generation mean and variance analysis to identify the gene activities responsible for regulating drought tolerance characteristics associated with groundnut growth and yield. Determining out how additive, dominance, and epistatic effects contributed to these features was the main goal of the study. In order to assess characteristics like days to maturity, biomass yield, pod yield, seed yield, harvest index, and others, the study examined a number of groundnut populations under well-watered (WW) and water-stressed (WS) conditions. Results showed that yield attributes and drought tolerance are highly influenced by both additive and non-additive gene activities. While epistatic interactions were significant for variables like days to maturity and harvest index, dominance effects were notably essential in determining yield and its components. High estimates of narrow-sense heritability were found for characteristics like dry biomass weight (96%) and number of seeds per plot (89%), which suggests strong additive genetic control. On the other hand, qualities with high broad-sense heritability (78% and 98%, respectively) and low narrow-sense heritability (78% and 12%, respectively) revealed significant non-additive genetic variance. The Chinese x Ndogba crossed F1 and F2 plants showed remarkable adaptability, according to the drought tolerance index (DTI), which indicated strong drought tolerance in particular generations.

Keywords: *Early-maturing; drought-tolerant; heritability; additive; dominance*

Article information
Received 1 September 2024;
Accepted 5 October 2024;
Published 12 November 2024
https://doi.org/10.26765/DRJAFS52372264

Citation Oppong-Sekyere, D., and Orlando, W.A. (2024). Determining the type of gene action(s) involved in the genetic control of drought-tolerance and yield-associated traits of groundnut (Arachis hypogaea L.) using generation mean and variance analysis of parental, F1 and the segregating populations (backcrosses and F2). Direct Research Journal of Agriculture and Food Science. Vol. 12(3), Pp. 73-93.

INTRODUCTION

Meteorological drought is characterized by low precipitation, which results in insufficient soil moisture, which causes crop damage and lower yields (Bodner et al., 2015; Dietz et al., 2021). Different crops are affected differently by meteorological drought, which varies by region and time period. Certain cereal crops, such as millet and sorghum, show drought tolerance, but more research is needed to understand their survival mechanisms. Cereals, like sorghum, in particular, thrive in low-rainfall and low-fertility marginal lands where other cereals fail (Mwadalu & Mwangi, 2013; Sakadzo & Kugedera, 2020). This C4 plant is highly efficient in hot and dry climates, maximizing the use of water and nutrients (Leakey et al., 2019). However, droughts brought on by global climate change still pose a threat to its performance due to insufficient moisture (Mukherjee et al., 2018).

In rain-fed regions including the Upper East, Upper West, and Northern part of Ghana, where drought has a major influence on agriculture, cultivating cultivars that combine early maturity and high yield is crucial to reducing the impact of drought on crops like groundnuts. In order to increase productivity, end-of-season drought, which is frequent in these regions, requires breeding for drought tolerance (Frahm et al., 2004; Khayatnezhad et al., 2011). Anjum et al. (2011) noted that a great deal of research has gone into understanding the physiological, morphological, and biochemical mechanisms of drought tolerance in crops like groundnuts and sorghum. Despite advancements, little is known about the precise mechanisms underlying sorghum's resistance to drought and steady grain yield. In light of the growing drought conditions predicted by climate change, multi-approach tactics are essential for identifying and utilizing characteristics that improve crop tolerance (Morales et al., 2020a).

Due to their effects on the ozone layer and decreased soil moisture, human activities including agriculture, industrialization, and urbanization intensify climate change and drought (Celik, 2020; Edo et al., 2024a). Breeding drought-resistant groundnut varieties requires characteristics such as transpiration efficiency, specific leaf area (SLA), and Soil-Plant Analytical Development (SPAD) Chlorophyll Meter Readings (SCMR) (Nigam and Aruna, 2008). According to Richardson et al. (2002) and Sheshshayee et al. (2006), SCMR is a dependable and non-invasive substitute for TE that provides information on the chlorophyll content and light-transmittance characteristics of leaves. Groundnut SLA and SCMR have been found to vary significantly in genetic research, while TE and SCMR have been found to positively correlate (Bindu Madhava et al., 2003; Sheshshayee et al., 2006).

The significance of SCMR's negative correlation with SLA has led to its proposal as a quick way to identify cultivars with high water-use efficiency (Nageswara et al., 2001; Upadhyaya, 2005). Moreover, SCMR and pod yield correlate, suggesting that it has application in breeding programs (Bindu Madhava et al., 2003). Correlations between harvest index, SLA and SCMR have been verified by studies on groundnut performance in drought and well-watered environments (Songsri et al., 2008). Studies on groundnut heritability have revealed high to moderate heritability for traits like SLA and SCMR, signifying the importance of additive gene effects and the potential for selection in breeding programs to improve drought tolerance and yield (John et al., 2011; Pasupuleti et al., 2015; Govardhan et al., 2018). Breeders can select exceptional characteristics by using their understanding of heritability in segregating populations to understand the genetics of hybridization and inbreeding (Ali and Wynne, 1994).

Successful selection based on additive genetic variance depends on heritability, or the fraction of phenotypic variance owing to genetic variation (Ogunniyan & Olakojo, 2014). Parent-offspring regression techniques, such as utilizing combinations like F1/F2, F2/F3, and F3/F4 in self-fertilizing crops, are commonly used to estimate heritability (Oppong-Sekyere et al., 2019). By using generation mean and variance analysis of parental, F1, and segregating populations (backcrosses and F2), this study seeks to identify the types of gene activities involved in the genetic control of drought-tolerance traits for growth-associated indicators.

MATERIALS AND METHODS

Experimental site and general evaluation activities

The hybridization activities (crosses) were carried out in the screen house of the Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, Bolgatanga, Upper East, Ghana, and beginning from 2nd August, 2022. Bi-parental crosses were made to develop F_1, F_2 and backcross generations. The field work comprising the assessment of parental lines (P_1 and P_2) and their F_1s, F_2s and BC generations was carried out between January and November, 2023 at the experimental fields of the Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, Bolgatanga, Upper East, Ghana.

Evaluation of crosses for populations (1 and 2) with their set of F_1, F_2, $BC_{1.1}$, $BC_{1.2}$ and their parents (P_1 and P_2), was carried out based on RCBD in four replications. Plot sizes adopted were 5 m x 2 m (10 m^2). F_1 crosses (hybrids) together with their backcrosses, male and female parents were put under field experiment based on two water regimes; well-watered (WW) and water-stressed (WS) conditions. Harvesting was done about 90 days after planting.

Before planting, the field was prepared, and all cultural activities carried out accordingly.

Data from observations for each generation were recorded on plants from (P_1, P_2, F_1, F_2, $BC_{1.1}$, and $BC_{1.2}$) selected at random among parents and crosses for each population and water regime (WW and WS).

Genetic material

The genetic materials that formed the parental lines included one farmers' preferred variety, Chinese (M) - an early maturing and drought-tolerant landrace variety selected by farmers from a participatory rural appraisal (PRA) study, and three other landraces, Sinkara (M), Ndogba (F) and Chaco-pag (F), selected from the germplasm screening. Other traits that informed the choice of these parental materials include high pod, seed and biomass yields, high yield reduction, harvest indices, shelling %, drought tolerant and farmer-preferred characteristics.

Mating Design, hybridization activities and evaluation of populations

The mating design adopted in the current study was the bi-parental mating design and the variance components method was employed to estimate variances and heritability among the groundnuts. Ndogba (F) and Chaco-pag (F) varieties constituted the female parental lines, while the Chinese (M) and Sinkara (M) varieties formed the male parental lines (Table 5 a). The male parents (Chinese and Sinkara) constituted the parents that were drought tolerant, whereas the female parents (Ndogba and Chaco-pag) were drought susceptible. For population one (Figure 1), Chinese (M) was crossed to Ndogba (F) to produce F$_1$ generations of Chinese x Ndogba. This F$_1$ was backcrossed to the male parent, Chinese to produce BC$_{1.1}$ generations. In a similar manner, the F$_1$s generated (Chinese x Ndogba) were also backcrossed to the susceptible female parent (Ndogba) to produce BC$_{1.2}$ population. Some of the F$_1$s (Chinese x Ndogba) produced in the first parental cross were advanced, through selfing, to generate F$_2$ segregating population (Figure 1).

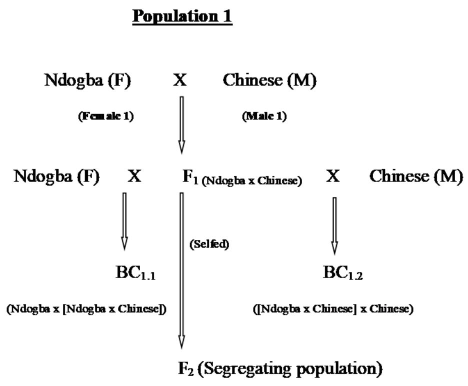

Figure 1: Design to generate the various populations for generation mean analysis (for Population 1).

For population two (Figure 1), the male parent, Sinkara (M), which was drought tolerant, was crossed to the drought-susceptible female parent, Chaco-pag (F) to produce F$_1$ population. The F$_1$ was then backcrossed to the drought-tolerant male parent, Sinkara to generate BC$_{1.1}$ individuals.

Crossing block layout for hybridization activities

The F$_1$ was again backcrossed to the drought susceptible female parent (Chaco-pag) to produce BC$_{1.2.}$ Some of the F$_1$s for population two (Sinkara x Chaco-pag) were advanced by selfing them to produce F$_2$ segregating population (Table 1 and Figure 2).

Table 1: Crossing block layout.

Females	Males
Ndogba	Chinese
Chaco-pag	Sinkara

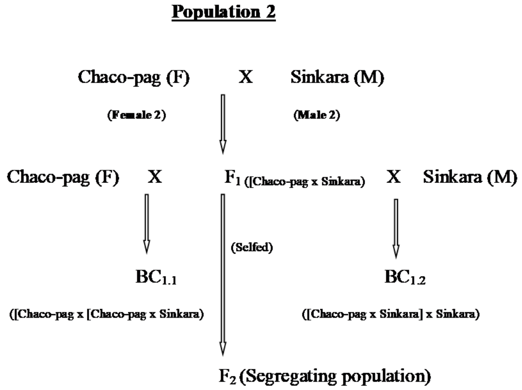

Figure 2: Design to generate the various populations for generation mean analysis (for Population 2).

To produce more hybrid seeds, each individual female underwent about eight crossings. Upon harvesting, every F1 plant was meticulously inspected for several morphological characteristics, including as height, color of leaves, pod, and seed characteristics, and their hybridity was verified by comparing them with both parents. In the first week of December 2022, the F1 crosses were harvested. September 2023 marked the completion of the F2 harvest. For prospective genetic research, the seeds of the two populations' BC1.1 and BC1.2, parents 1 and 2,
F1s, and F2s were preserved.

Generation mean and variance analysis for groundnut populations under well-watered and water-stressed conditions

At the experimental fields of the Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, Bolgatanga, Upper East, Ghana, six generations (P1, P2, F1, F2, BC1.1, and BC1.2) of groundnut populations were sown in the 2023 season. To reduce inter-genotypic concurrence and sufficiently explore genetic variability, the experimental setup consisted of two ridges for each parent and F1 plant, seven ridges for backcrosses, and twelve ridges for F2 plants. Twenty plants were trimmed to one plant per hill, with each ridge measuring 60 cm in width and 20 cm apart. Two water regimes—well-watered (WW) and water-stressed (WS)—were used to test the groundnut generations. The following parameters were measured: days to 50% emergence, days to 50% flowering, plant height at flowering and harvest, fresh and dry biomass weight, number of pods per plot, pod weight, number of seeds per plot, seed weight, days to maturity, harvest index, SCMR at 60 and 80 DAP, and drought tolerance index. Data were collected from 20, 20, 25, 200, 120, and 120 plants from P1, P2, F1, F2, BC1.1, and BC1.2, respectively. The methods by Upadhyaya et al. (2011) and Kakeeto et al. (2020) were followed during the measurements.

Harvest Index (HI) was estimated using the formula:

Harvest Index (HI): $\frac{Economic\ yeild}{Total\ Biomass\ (haulm)\ Weight}$

(Mukhtar et al., 2013; Bhatt et al., 2020)
(www.fao.org/docrep/004/Y3655E/y3655e07.hmt).

SPAD (soil plant analysis development) - chlorophyll meter reading at 60 and 80 DAP (SCMR) (relative chlorophyll content or greenness of leaves)

According to Nageswara et al. (2001), plants were sampled at random, and in the morning (09:00 AM ± 12:00 PM), the second completely developed leaf from the top of the main stem was utilized for SCMR assessment. The chlorophyll concentration was recorded on each of the four leaflets of the tetrafoliate leaf. Twenty single observations (four leaflets x five plants per plot) were used to calculate the average SCMR for each plot (Arunyanark et al., 2008). During the SCMRs, great care was taken to make sure the SPAD meter sensor covered the whole leaf lamina to avoid interference from veins and midribs.

Drought tolerance index (DTI)

As recommended by Oppong-Sekyere et al.(2019) and Jin et al. (2019) each trait's definition was determined as the ratio of the trait value—for example, pod yield—measured under water-stressed (WS) conditions over the value recorded under well-watered conditions (WW). Consequently, DTI was calculated for the following traits: HI, biomass (dry weight), number of pods per plot, SCMR 60 and 80 DAP, and number of pods. A genotype that is drought tolerant has a DTI > 1. DTI < 1 indicates that the genotype is not resistant to drought (Oppong-Sekyere et al., 2019; Jin et al., 2019).

Statistical and genetic analysis

The GenStat statistical program (Discovery Edition 6) was used to examine the trait data using an ANOVA. Using the GenStat statistical program (Discovery Edition 4), characteristics data were analyzed using the ANOVA method. To identify any significant variations between the means of the several generations, the Standard Error of the Difference (SED) was set at 5%. The mean squares of the traits from the ANOVA among the groundnut crosses for the two (2) water regimes were computed, along with correlations between the genotypes of groundnuts.

Generation mean analysis was conducted using Mather's (1949) scaling tests A, B, and C, along with Cavalli's joint scaling test (Cavalli, 1952). These tests, performed using the 'R' statistical software and Plant Breeder's Tools, aimed to determine the genetic control of various yield and yield-associated traits, such as harvest index, pod and seed numbers, biomass yield, and maturity traits. The A, B, and C tests evaluated the adequacy of the additive-dominance model by checking for significant deviations from zero and Chi-square (X^2) values (Kabbia et al., 2017).

The model was considered adequate if all values were zero, but significant deviations indicated complex genetic factors like non-allelic interactions or epistasis. Cavalli's joint scaling test was used in such cases, along with log-transformation to normalize the data (Mather & Jinks, 1982).

Significance of A, B, and C was determined by t-tests, with non-allelic gene interactions inferred when these tests were significant (Kabbia et al., 2017).

Cavalli's joint scaling test has the advantage of testing goodness of fit once instead of in three separate instances and of making clear at once, if the fit is bad; which part of the data is responsible for it (Kabbia *et al.*, 2017).

The generation means were influenced by three key parameters: 'm' (mid-parent value), [d] (additive components), and [h] (dominance components), as estimated through a generalized inverse matrix equation ($M = J^{-1}S$). This method uses the weighted least-squares value of m, [d], and [h], with weights being the reciprocal of the variance of the generation means (1/Vx). The expected generation means were then calculated using these weighted values (Mohamed, 2014; Wannows et al., 2015; Kabbia et al., 2017). The comparison between observed and expected values was performed by minimizing the sum of squares, distributed as Chi-square (X^2), with degrees of freedom equal to the number of generation means minus the number of fitted parameters (Kabbia et al., 2017).

Scaling tests (A, B and C) results interpretation

The expected mean of any generation is directly related to the parental and F1 means, assuming that the generation mean depends solely on additive x dominance effects (Kearsey & Pooni, 1996). When $p > 0.05$, scaling tests A, B, and C are not significantly different from zero, indicating that the additive-dominance model is adequate for explaining mean variations and suggesting that complicating factors like maternal effects and non-allelic gene interactions are absent (Kearsey & Pooni, 1996). Conversely, if $p < 0.05$, scaling tests A, B, and C significantly deviate from zero, indicating that the additive-dominance model alone is insufficient. This suggests the presence of complicating factors such as maternal effects or gene interactions like epistasis. In such cases, further analysis with additional regression variables and simple linear regression is necessary to better fit the additive-dominance model (Kearsey & Pooni, 1996). Simple linear regression model that was fitted is as follows;

$$Y = m + b_1 x_a + b_2 x_d + E$$

Where;
Y = Expected generation mean. m = Intercept, b_{x1} *= Coefficient of net additive,* x_a *= Net additive effect,* b_2 *= Coefficient of net dominant,* x_d *= Net dominant effect and E = Unexplained experimental error.*

Regression model interpretation

Where $p < 0.05$ and the intercept, net additive and dominant effects are deemed significant and the model therefore fits adequately and is able to explain the variation in the traits of the generations. However, where $p > 0.05$ and any of the intercept, net additive and dominant effects is considered not significant or even when one of them is significant and the others are not, a new model is fitted to ensure the adequacy of the additive-dominance model (Kearsey and Pooni, 1996).

Joint scaling test results

In the joint scaling tests, where both parameters are significant but the calculated chi-square value is not significant as compared to the critical chi-square value (3.841), and then the model is considered inadequate. In this case, a new model is fitted so that the chi-square value declares non-significance (Kearsey and Pooni, 1996).

Estimation of heritability: the variance component method

The statistical procedure of analysis of variance (ANOVA) for Bi-parental mating design (Figure 2) was used in the estimation of variances and subsequently in the estimation of heritability (narrow and broad-sense) of the various groundnut components. In the estimation of heritability, in which the variance component method was adopted, the total variance of a quantitative trait for F_2 was mathematically expressed as follows:

$$V_P = V_G + V_E + V_{GE}$$

Where V_P = total phenotypic variance of the segregating population, V_G = genetic variance, V_E = environmental variance, and V_{GE} = variance associated with the genetic (genotype) and environmental interaction.
The genetic component of variance was further partitioned into three components as follows:

$$V_G = V_A + V_D + V_I$$

Where; V_A = additive variance (variance from additive gene effects), V_D = dominance variance (variance from dominance gene action), and V_I = interaction (variance from interaction between genes, epistatic).

Additive genetic variance is the variance of breeding value and it is the primary cause of resemblance between relatives. Hence, V_A is the primary determinant of the observable genetic properties of the population, and of the response of the population to selection. Further, V_A is the only component that the researcher can most readily estimate from observations made on the population.

The total phenotypic variance may then be rewritten as:

$$V_P = V_A + V_D + V_I + V_E + V_{GE}$$

Heritability estimate using basic generations was as follows:

$$V_{F2} = V_A + V_D + V_E = Vp$$

$$V_{B1} + V_{B2} = V_A + 2V_D + 2V_E$$

$$V_E = \frac{(V_{P1} + V_{P2} + V_{F1})}{3}$$

$$H^2 = \frac{(V_A + V_D)}{(V_A + V_D + V_E)} = \frac{V_G}{V_P}$$

$$h^2 = \frac{(V_A)}{(V_A + V_D + V_E)} = \frac{V_A}{V_P}$$

$$V_A = 2V_{F2} - (V_{B1} + V_{B2})$$

$V_D = [(V_{B1} + V_{B2}) - F_2 - V_E$

Estimation of heritability from the generation mean analysis of the six (6) generations of the groundnut populations connotes that,

VP_1 = Variance of Parent 1.
VP_2 = Variance of Parent 2.
VF_1 = Variance of F_1 progenies
VF_2 = Variance of F_2 progenies
$VBC_{1.1}$ = Variance of Backcross progenies to parent 1
$VBC_{1.2}$ = Variance of Backcross progenies to parent 2.

Based on the components of genetic variance from the populations above, including the dominance (σ^2_D), additive (σ^2_A) and environmental variances (σ^2_E), the heritability estimates for narrow-sense (h^2_n) and broad-sense (H^2_b) were calculated for the individual groundnut traits based on the formulae below:

Broad-sense heritability (H^2)

Heritability estimated using the total genetic variance (V_G), called broad-sense heritability was expressed mathematically as:

$$H^2 = \frac{V_G}{V_P}$$

Narrow-sense heritability (h^2)

Because the additive component of genetic variance determines the response to selection, the narrow sense heritability estimate is more useful to plant breeders than the broad sense estimate. It was therefore expressed as:

$$h^2 = \frac{V_A}{V_P}$$

RESULTS AND DISCUSSION

Components of variation (heritability) for different groundnut traits (using F2 and BC populations)

The study on groundnut traits revealed significant insights into the genetic architecture of drought tolerance (Table 2). Heritability estimates varied widely, with narrow-sense heritability (h^2) ranging from 7% to 96%. Traits like dry biomass weight (96%) and number of seeds per plot (89%) exhibited high h^2, indicating strong additive genetic control, which aligns with findings by Fonceka et al. (2012) and Pandey et al. (2014). High heritability suggests effective selection for these traits. Conversely, traits such as harvest index and number of pods per plot had low h^2 (7% and 12%) but high broad-sense heritability (H^2) of 78% and 98%, reflecting significant non-additive genetic variance. This is consistent with Nigam et al. (2001), who observed similar patterns, emphasizing the roles of dominance and epistasis. Scaling test results for pod and seed numbers showed significant differences, indicating the inadequacy of the additive-dominance model under both well-watered (WW) and water-stressed (WS) conditions. Non-allelic interactions such as additive x additive and dominance x dominance suggest complex genetic control, aligning with Upadhyaya et al. (2001), who reported similar findings in groundnut yield traits. The higher net additive effects compared to dominance effects indicates the crucial role of additive genetic variance.

For days to 50% plant emergence, significant non-allelic gene interactions were observed under WW but not WS conditions. The negative values for net additive x additive and net dominance effects suggest recessive alleles for earlier emergence, supporting Hamidou et al. (2012), who also found over-dominance in stress conditions. Days to 50% flowering showed significant non-allelic interactions under both conditions, with negative effects, indicating over-dominance for earlier flowering traits.

Days to maturity exhibited significant non-allelic interactions, with dominance effects being more substantial than additive effects, consistent with Holbrook et al. (2009). This supports the importance of dominance in maturation traits.

Generally, groundnuts under WW conditions performed better compared to WS, emphasizing the impact of water availability on growth and development, as noted by Bhatnagar-Mathur et al. (2007). The high heritability for key traits under both conditions underscores the potential for breeding drought-tolerant varieties through selective breeding, incorporating both additive and dominance effects.

Generations under well-watered (WW) and water-stressed (WS) Conditions

The scaling tests A, B, and C (Mather, 1949) showed no significant differences from zero ($P \geq 0.05$) for harvest index (HI) in groundnut generations under both well-watered (WW) and water-stressed (WS) conditions. This indicates that the additive-dominance model was sufficient to explain the variation in HI across generations. The mid-parent value of HI was 0.519 (WW) and 0.49 (WS), with a net additive effect of 0.16 (WW) and 0.17 (WS) and a negative net dominance effect of -0.077 (WW) and -0.015 (WS). The negative dominance values suggest gene dispersion in the parent plants, leading to small additive effects. This indicates the presence of decreasing alleles responsible for HI in the

Table 2: Components of variation (Heritability) for different groundnut traits (using F2 and BC Populations).

Traits	Mean	MSg	MSe	σ^2_A	σ^2_D	σ^2_p	σ^2_g	σ^2_e	h^2_n	H^2_b
Days to 50% emergence	7.08	0.49	0.28	0.88	0.00	1.36	0.88	0.47	0.65	0.65
Days to 50% flowering	25.58	5.78	4.61	4.00	5.20	11.50	9.20	2.30	0.35	0.80
Days to maturity	89.17	10.80	1.38	3.68	3.84	8.73	7.52	1.21	0.42	0.86
Plant height at flowering	15.42	22.37	7.98	32.72	56.60	91.56	89.32	2.24	0.36	0.98
Plant height at harvesting	47.37	103.46	105.34	220.46	498.60	729.30	719.06	10.24	0.30	0.99
No of pods per plot	44.62	2525.12	40.19	22.88	159.04	186.35	181.92	4.43	0.12	0.98
Pod weight	427.71	133912.92	9127.25	32485.26	51906.68	84445.61	84391.94	53.67	0.38	0.99
No. of seeds per plot	86.00	2909.77	129.11	437.32	40.20	485.93	477.52	8.41	0.89	0.98
Seed weight	388.27	184715.46	7711.24	46369.18	20810.36	672298.87	67178.54	50.33	0.69	0.99
Fresh biomass	559.81	174693.44	18450.51	38952.54	26842.88	65904.70	65795.42	109.28	0.59	0.99
Dry biomass	327.98	62900.28	3082.82	8172.44	317.68	8537.48	8490.12	47.36	0.96	0.99
Harvest Index (HI)	0.27	0.0024	0.0029	0.01	0.104	0.146	0.114	0.032	0.07	0.78
SCMR60DAP	22.40	106.94	97.94	147.74	342.58	501.53	490.32	11.21	0.29	0.98
SCMR80DAP	28.30	64.21	35.81	138.18	74.36	218.60	212.54	6.06	0.63	0.97

MSg = Mean sum of squares due to genotypes, MSe = Mean sum of squares due to error, σ^2p = Phenotypic variance, σ^2g = Genotypic variance, σ^2e = Environmental variance, h^2_n = Heritability in the narrow sense, H^2_b = Heritability in broad sense.

groundnut genotypes. Negative values for both additive [d] and dominance [h] effects were observed for HI under both water conditions, suggesting that alleles for low-value traits were dominant over those for higher-value traits. The opposing directions of additive and dominance effects, indicated by their non-parallel signs, were consistent under both WW and WS conditions, highlighting a complex interaction between additive and dominance gene effects for HI in these groundnut varieties. These results are further demonstrated by recent research. As per Jadhav et al. (2023), there is a correlation between lower allelic contributions to yield traits in legumes and gene dispersion when it comes to negative dominance effects. Kumar et al. (2022) discovered that gene dispersion influences harvest index through diminished additive effects in situations that are water-stressed. Furthermore, as noted by Patel et al. (2024a), negative dominance effects may be suggestive of gene loss or dispersal, which is consistent with the genotype results reported for groundnuts.

Pod number

The scaling test results for the number of pods per plot under well-watered (WW) conditions revealed a significant difference from zero ($P < 0.05$), indicating that the additive-dominance model alone could not explain the variation among the groundnut crosses. The significance of all three scaling tests (A, B, and C) suggested the presence of complex genetic interactions, including additive x additive (i), additive x dominance (j), and dominance x dominance (l) gene interactions. This indicates that maternal effects and non-allelic gene interactions contributed to pod yield under WW conditions (Tables 3a and b). In the water-stressed (WS) environment, only scaling test A showed a significant difference, again pointing to the presence of all three types of gene interactions in the groundnut crosses. The mid-parent value, net additive, net dominance, and other gene effects under WW were not drastically different from those observed under WS conditions. Pod yield was influenced by dominance x dominance gene action in both water regimes. Notably, the net additive effect was greater than the net dominance effect for both WW (0.1614) and WS (0.173), while net dominance values were negative, indicating a gene dispersion effect (WW: -0.0769, WS: -0.0154). These results highlight the complex genetic control of pod yield in groundnuts under different water conditions. These results correlate with the results of recent research. Similar gene interaction patterns influencing pod production in legumes were observed by Singh et al. (2023), with non-allelic interactions being critical. According to Patel et al. (2024a), yield attributes under different water conditions are considerably influenced by both additive and non-additive gene effects. Furthermore, Chen et al. (2022) provided

Table 3 a: Generation Mean Analysis of Harvest Index (HI) under Well-Watered (WW) and Water-Stressed (WS)

Harvest Index (WW)				
	Estimate	**SE**	**T-test**	**P- value**
Scaling test A	0.1483	0.1356	1.0933	0.2759
Scaling test B	0.1311	0.1466	0.8941	0.3726
Scaling test C	-0.1098	0.2269	-0.4838	0.6289
Joint scaling test: Regression Model: mean ~ m + a + d				
Regression Coefficients				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
M	0.519	0.0866	5.9968	0.1052
[a]	0.1614	0.0577	2.7949	0.2187
[d]	-0.0769	0.1482	-0.5192	0.6951
Residual Standard Error	0.7098			
Multiple R-square	0.9992			
Adjusted R-square	0.9951			
F-value	244.2642			
p-value	0.0485			
Observed and Predicted Values of Generation Means				
Generation	**Observed**	**Predicted**		
P_1	0.794	0.764914		
P_2	0.462	0.442181		
F_1	0.492	0.442095		
F_2	0.4876	0.480569		
$BC_{1.1}$	0.4714	0.482274		
$BC_{1.2}$	0.5076	0.521117		
Chi-square value:	0.503799			
Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action p-value:	0.477836			

Table 3 a: Contd.

Harvest Index (WS)				
	Estimate	**SE**	**T-test**	**P value**
Scaling test A	-0.3432	0.1881	-1.8241	0.07
Scaling test B	0.0612	0.1778	0.3443	0.7311
Scaling test C	-0.2896	0.3114	-0.9298	0.3533
Joint scaling test Regression Model: mean ~ m + a + d Regression Coefficients				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	0.4921	0.0527	9.3348	0.0679
[a]	0.173	0.0323	5.3567	0.1175
[d]	-0.0154	0.0946	-0.1629	0.8972
Residual Standard Error	0.405			
Multiple R-square	0.9997			
Adjusted R-square	0.9984			
F-value	750.6887			
p-value	0.0277			
Observed and Predicted Values of Generation Means				
Generation	**Observed**	**Predicted**		
P_1	0.794	0.780579		
P_2	0.462	0.434564		
F_1	0.492	0.476648		
F_2	0.4876	0.484356		
$BC_{1.1}$	0.4714	0.476418		
$BC_{1.2}$	0.5076	0.515916		
Chi-square value	0.16402			
p-value	0.685482			

evidence that dominant × dominant interactions are common in stressed crops, supporting the dominance effects seen in groundnuts.

Seed number

The scaling test results for the number of seeds per plot indicated a significant difference from zero at $P < 0.05$ under well-watered (WW) conditions for groundnut crosses (Table 3c). All scaling tests (A, B, and C) showed significant deviations from zero, meaning the additive-dominance model alone could not explain the observed variation. This suggests the presence of complicating factors such as maternal effects and gene interactions (epistasis or non-allelic gene interaction) among the groundnut crosses in the well-watered environment.

Table 3 b: Generation Mean Analysis of Number of Pods per Plot

POD NUMBER (WW)				
	Estimate	**SE**	**T_test**	**P value**
Scaling test A	-28.2211	0.4472	-63.1043	0
Scaling test B	-18.6002	0.387	-48.0576	0
Scaling test C	-78.1615	0.6614	-118.183	0
Joint scaling test Regression Model: mean ~ m + a + d + aa + dd				
Regression Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
M	3.9429	7.8641	-0.5014	0.7041
[a]	1.2722	2.0091	0.6332	0.6406
[d]	63.5374	21.219	2.9944	0.2052
[aa]	31.4177	6.6915	4.6952	0.1336
[dd]	13.6163	15.1346	0.8997	0.5336
Residual Standard Error	18.4706			
Multiple R-square	0.9996			
Adjusted R-square	0.9974			
F-value	453.8668			
p-value	0.0356			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	33.3295	28.74701		
P_2	23.33	26.20266		
F_1	73.2108	73.2108		
F_2	31.2299	31.2299		
$BC_{1.1}$	39.1596	39.72041		
$BC_{1.2}$	38.9703	38.44823		
Chi-square value:	341.1635			
p-value:	3.56E-76			

Table 3 b: Contd.

POD NUMBER (WS)	**Estimate**	**SE**	**Test**	**P value**
Scaling test A	0.0251	0.01	2.51	0.0131
Scaling test B	-0.2812	0.01	-28.12	0
Scaling test C	-0.7863	0.0141	-55.5998	0
Joint scaling test: Regression Model: mean ~ m + a + d + aa + ad				
Regression Coefficients:				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
M	4.9666	1.6885	2.9414	0.2086
[a]	1.118	1.1782	0.9489	0.5167
[d]	60.9741	2.8701	21.2447	0.0299
[aa]	22.6795	1.8563	12.2178	0.052
[ad]	13.5048	2.9613	4.5604	0.1374
Residual Standard Error	7.0657			
Multiple R-square	0.9999			
Adjusted R-square	0.9997			
F-value	3450.331			
p-value	0.0129			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	29.3095	28.76405		
P_2	26.9815	26.52812		
F_1	66.78	65.94077		
F_2	35.5999	35.4537		
$BC_{1.1}$	44.7904	45.05875		
$BC_{1.2}$	36.8804	37.18838		
Chi-square value:	49.92445			
p-value:	1.60E-12			

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action

The significance of all three scaling tests in the WW condition suggests the existence of all three types of non-allelic gene interactions: additive x additive (i), additive x dominance (j), and dominance x dominance (l) for the seed yield trait (Table 3c). In the water-stressed (WS) environment, all three scaling tests also showed significant differences from zero at $P < 0.05$, indicating that the additive-dominance model was insufficient to

Table 3 c: Generation Mean Analysis of Number of Seeds/Plot

SEED NUMBER (WW)				
	Estimate	**SE**	**T_test**	**P value**
Scaling test A	21.0584	0.3838	54.8686	0
Scaling test B	22.7492	0.4263	53.369	0
Scaling test C	-69.9318	0.7029	-99.4973	0
Joint scaling test Regression Model: mean ~ m + a + d + aa + ad				
Regression Coefficients				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
M	16.8815	41.8424	0.4035	0.7559
[a]	6.6866	23.9659	0.279	0.8268
[d]	99.8699	68.0889	1.4668	0.3809
[aa]	56.1563	46.1765	1.2161	0.4381
[ad]	22.6567	66.3229	0.3416	0.7904
Residual Standard Error	181.4553			
Multiple R-square	0.9899			
Adjusted R-square	0.9396			
F-value	19.6634			
p-value	0.1695			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	68.9895	79.72441		
P_2	59.8095	66.35127		
F_1	99.7596	116.7514		
F_2	61.8704	66.81643		
$BC_{1.1}$	97.9398	89.86297		
$BC_{1.2}$	79.5097	71.84807		
Chi-square value:	32926.02			
p-value:				0

Table 3 c: Generation Mean Analysis of Number of Seeds/Plot

	Estimate	**SE**	**T test**	**P value**
Scaling test A	1.167	5.00E-04	2527.478	0
Scaling test B	1.293	0.0276	46.8342	0
Scaling test C	-3.7969	0.0332	-114.529	0
Joint scaling test, Regression Model: mean ~ m + a + d + aa + ad				
Regression Coefficients:				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
m	1.8831	1.5648	1.2034	0.4414
[a]	0.7002	0.3402	2.0585	0.2879
[d]	15.8249	3.9334	4.0232	0.1551
[aa]	6.2078	1.4698	4.2236	0.148
[ad]	-7.7202	2.6663	-2.8955	0.2117
Residual Standard Error	65.2624			
Multiple R-square	0.9997			
Adjusted R-square	0.998			
F-value	613.7846			
p-value	0.0306			
Observed and Predicted Values of Generation Means				
Generation	**Observed**	**Predicted**		
P_1	8.305811	8.791083		
P_2	7.733523	7.39065		
F1	9.987869	9.987869		
F_2	7.865513	7.865513		
$BC_{1.1}$	9.896325	9.767568		
$BC_{1.2}$	8.91666	9.067352		
Chi-square value:	4259.177			
p-value:				0

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action.

explain the seed yield variation in this condition as well. The results indicated that the additive x dominance gene effect played a major role in the groundnut crosses, with the net dominance effect being significantly larger than the net additive effect in both WW (99.89) and WS (15.82) conditions. The mid-parent value was also higher for WW (16.88) compared to WS (1.88). For WW, the net additive x additive gene effect (56.16) was greater than the net additive x dominance gene effect (22.66), while the WS condition displayed a similar pattern (6.21; -7.72). The negative net additive x dominance value under WS suggests gene dispersion, with decreasing alleles affecting seed yield. Negative values for non-allelic interactions (additive x dominance) indicate that lower-

Table 3 d: Generation Mean Analysis of Biomass yield

BIOMASS (DRY) (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	0.0455	4.00E-04	106.6421	0
Scaling test B	-0.0177	4.00E-04	-41.315	0
Scaling test C	-0.2832	7.00E-04	-391.933	0
Joint scaling test: Regression Model: mean ~ m + a + d + aa + dd				
Regression Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
M	1.7246	0.1377	12.5215	0.0507
[a]	0.0805	0.0313	2.5733	0.236
[d]	1.7174	0.3545	4.8441	0.1296
[aa]	0.5975	0.1188	5.0305	0.1249
[dd]	-0.8284	0.2356	-3.5157	0.1764
Residual Standard Error	213.6659			
Multiple R-square	1			
Adjusted R-square	0.9998			
F-value	7297.111			
p-value	0.0089			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	2.357742	2.4025		
P_2	2.333259	2.241577		
F_1	2.613534	2.613534		
F_2	2.376153	2.376153		
$BC_{1.1}$	2.571754	2.565756		
$BC_{1.2}$	2.476961	2.485294		
Chi-square value:	45653.11			
p-value:				0

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action

value traits were dominant over higher-value traits. The opposite gene effects, with non-parallel signs, suggest duplicated types of non-allelic interaction (epistasis) in these traits (Table 3c).

Biomass yield

All the three scaling tests (A, B, and C) for biomass yield (fresh and dry) in the current study proved significantly ($p < 0.05$) different from zero for both well-watered and water-stressed environments (Table 3d). Thus, the additive-dominance model alone was not adequate to explain the variation among the means. Therefore, the complicating factors including maternal effects and interactions between genes (epistasis) exist among the groundnut traits under both water conditions for biomass yield. This suggests the presence of all three types of non-allelic gene interactions: additive x additive (i), additive x dominance (j) and dominance x dominance (l) among the groundnut crosses for biomass yield trait across both environments (Table 3d). Estimates from the joint scaling test for dry biomass yield for well-watered (WW) environment shows that, net dominance x dominance gene action was at play and that the estimate revealed a negative value (-0.83) which suggests the genes for biomass yield under WW were in dispersion; the estimated additive effect was thus small (0.08). This indicates decreasing alleles for the biomass trait in the genotype. A similar trend was observed under WS conditions though the sign for the net dominance x dominance effect was positive (0.019). Net dominance effect was larger than net additive gene effects in both water regimes. Under water-stressed condition, the net mid-parent value (2.4572) was positive and significant at p = 0.022, which shows that the trait is quantitatively inherited (Table 3d).

Plant emergence

The scaling test results for the number of seeds per plot indicated a significant difference from zero at $P < 0.05$ under well-watered (WW) conditions for groundnut crosses (Table 3e). All scaling tests (A, B, and C) showed significant deviations from zero, meaning the additive-dominance model alone could not explain the observed variation. This suggests the presence of complicating factors such as maternal effects and gene interactions (epistasis or non-allelic gene interaction) among the groundnut crosses in the well-watered environment. The significance of all three scaling tests in the WW condition suggests the existence of all three types of non-allelic gene interactions: additive x additive (i), additive x dominance (j), and dominance x dominance (l) for the seed yield trait (Table 3e).

Table 3 e: Generation mean analysis of days to 50% Emergence

EMERGENCE (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	0.0168	0.07	0.2406	0.8102
Scaling test B	-0.1947	3.00E-04	-692.859	0
Scaling test C	0.1743	0.1104	1.5791	0.1155
Joint scaling test Regression Model: mean ~ m + a + d + aa + dd				
Regression Coefficients:				
	Estimate	Std. Error	t-value	Pr(>|t|)
M	11.5709	1.1546	10.022	0.0633
[a]	0.2597	0.2702	0.9614	0.5125
[d]	-9.6326	3.0499	-3.1584	0.1952
[aa]	-3.946	1.0857	-3.6345	0.1709
[dd]	5.0617	2.3094	2.1918	0.2725
Residual Standard Error	2.7415			
Multiple R-square	0.9997			
Adjusted R-square	0.9983			
F-value	716.4508			
p-value	0.0284			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	8.1	7.884585		
P_2	7	7.36511		
F_1	7	7		
F_2	8.02	8.02		
$BC_{1.1}$	7.0333	7.163362		
$BC_{1.2}$	7.025	6.903625		
Chi-square value:	7.51565			
p-value:	0.006116522			

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action

Table 3 e Contd: Generation mean analysis of days to 50% Emergence

EMERGENCE (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	-1.0334	0.3633	-2074.36	0
Scaling test B	0.05	0.3882	0.1288	0.8977
Scaling test C	2.98	0.6494	4.589	0
Joint scaling test Regression Model: mean ~ m + a + d + aa + dd				
Regression Coefficients:				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	2.8923	0.2104	13.7471	0.0462
[a]	0.1719	0.0513	3.3482	0.1848
[d]	-0.78	0.5495	-1.4195	0.3907
[aa]	-0.3333	0.1925	-1.7314	0.3334
[dd]	0.514	0.3712	1.3848	0.3981
Residual Standard Error	2.3953			
Multiple R-square	0.9999			
Adjusted R-square	0.9996			
F-value	2842.893			
p-value	0.0142			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	Observed	2.730915		
P_2	2.654524	2.387077		
F_1	2.441672	2.626246		
F_2	2.626246	2.630748		
$BC_{1.1}$	2.630748	2.633393		
$BC_{1.2}$	2.648809	2.461474		
Chi-square value:	2.436634			
p-value:	5.7375			

In the water-stressed (WS) environment, all three scaling tests also showed significant differences from zero at $P < 0.05$, indicating that the additive-dominance model was insufficient to explain the seed yield variation in this condition as well. The results indicated that the additive x dominance gene effect played a major role in the groundnut crosses, with the net dominance effect being significantly larger than the net additive effect in both WW

(99.89) and WS (15.82) conditions. The mid-parent value was also higher for WW (16.88) compared to WS (1.88).

For WW, the net additive x additive gene effect (56.16) was greater than the net additive x dominance gene effect (22.66), while the WS condition displayed a similar pattern (6.21; -7.72). The negative net additive x dominance value under WS suggests gene dispersion, with decreasing alleles affecting seed yield. Negative values for non-allelic interactions (additive x dominance) indicate that lower-value traits were dominant over higher-value traits. The opposite gene effects, with non-parallel signs, suggest duplicated types of non-allelic interaction (epistasis) in these traits (Table 3e).

Plant flowering

The results for days to 50% flowering showed no significant difference under well-watered (WW) conditions, with Mather's scaling test C yielding p = 0.1155. This suggests the presence of dominance x dominance (l) non-allelic gene interaction among the groundnut crosses, as at least one of the scaling tests was significant (Table 3f). In the water-stressed (WS) environment, scaling test A showed no significance (p = 0.8023). However, scaling tests B and C were significant, indicating the presence of all three types of gene interactions: additive x additive (i), additive x dominance (j), and dominance x dominance (l) (Table 3f). The joint scaling test results for days to 50% flowering followed a similar trend to that observed for days to 50% plant emergence. For both WW and WS conditions, the net additive effect (WW: -0.1205, WS: -0.1303) and the net dominance x dominance gene effect (WW: -1.8118, WS: -2.0952) showed negative values, suggesting gene dispersion and decreasing alleles for the trait responsible for days to flowering (Table 3f). The negative values for dominance x dominance [l] interactions indicate that alleles responsible for lower trait values were over-dominant compared to those controlling higher trait values. The opposing effects of additive and dominance x dominance genes, with non-parallel signs, suggest a duplicated type of non-allelic interaction (epistasis) in these traits (Table 3f).

Days to maturity

Mather's scaling test for days to plant maturity indicated no significant difference under well-watered (WW) conditions, with a p-value of 0.6984 for scaling test C (Table 3g). However, the significance of scaling tests A and B suggests the presence of all three types of non-allelic gene interactions: additive x additive (i), additive x dominance (j), and dominance x dominance (l). Under the water-stressed (WS) treatment, scaling test B also showed no significance (p = 0.7043). Similar to the well-watered conditions, the significance of scaling tests A and C indicates the existence of the same three types of gene interactions (Table 3g). Joint scaling test estimates revealed a negative net dominance x dominance gene effect (-0.6753) under WW conditions and -12.8174 under WS conditions, suggesting gene dispersion and decreasing alleles for the traits responsible for days to plant maturity.

The net dominance gene effect was greater (1.2266) than the net additive gene effect (0.1241) in WW conditions, consistent with findings under WS conditions where the net dominance was 23.272 and the net additive effect was 2.3675. The mid-parent values were positive and significant for both water conditions: WW (8.9881) with p = 0.011 and WS (80.5427) with p = 0.0234, indicating that the traits were quantitatively inherited (Table 3g).

Generation mean analysis for drought and yield-associated traits

Understanding the genetic mechanism controlling the desired trait is essential to selecting an effective breeding process. The harvest index trait's scaling tests (A, B, and C) were all found to be non-significant (P > 0.05) in accordance with the Mather (1949) method for calculating the scaling tests for the relevant parameters. This suggests that the basic additive-dominance model was sufficient to explain the variation in the harvest index means and to estimate the genetic components of trait variance (HI). This demonstrates that selection could be used to improve yield-associated traits in the segregating population (F2 generation) through appropriate selection practices (Kabbia et al., 2017).

But in the crosses, every scale (A, B, and C) or at least one of them was significantly (P < 0.05) different from zero (or equal to zero) for the traits: biomass yields, days to 50% emergence, days to 50% flowering, and days to plant maturity under WW and WS environments. Therefore, the majority of the genetic variation pertaining to the appearance of those traits could not be well explained by the additive-dominance model alone. This indicates that the inheritance of these traits may have been complicated and polygenic, as complicating variables including maternal effects and gene interaction (epistatic effects or non-allelic gene interaction) may have played a role.

These results are similar to those reported by Warnock *et al*. (1998) and Kabbia *et al*. (2017) in their generation mean and variance analysis studies for yield and yield associated traits in groundnuts.

Thus, it can be concluded that all three forms of non-allelic gene interactions—additive x additive (i), additive x dominance (j), and dominance x dominance (l)—were present in the groundnut generations (crosses) that exhibited the aforementioned features. Therefore, selection for improvement among the groundnut may

Table 3 f: Generation Mean Analysis of Days to 50% flowering

EMERGENCE (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	0.4061	0.039	10.408	0
Scaling test B	0.9289	0.0405	3306.493	0
Scaling test C	0.5398	0.0639	1.5791	0.1155
Joint scaling test Regression Model:	mean ~ m + a + d + aa + dd			
Regression Coefficients:				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	3.7967	0.9478	4.0057	0.1557
[a]	-0.1205	0.2162	-0.5574	0.6763
[d]	3.1097	2.4066	1.2921	0.4193
[aa]	1.0641	0.8795	1.2099	0.4397
[dd]	-1.8118	1.588	-1.1409	0.4582
Residual Standard Error	20.842			
Multiple R-square	0.9996			
Adjusted R-square	0.9978			
F-value	555.251			
p-value	0.0322			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	4.998993	4.740331		
P_2	4.689203	4.981377		
F_1	5.09461	5.09461		
F_2	4.898607	4.898607		
$BC_{1.1}$	5.001242	5.104379		
$BC_{1.2}$	5.291522	5.224902		
Chi-square value:	434.3877			
p-value:	1.80E-96			

Table 3 f Contd: Generation Mean Analysis of Days to 50% flowering

EMERGENCE (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	-0.0911	0.3633	-0.2508	0.8023
Scaling test B	0.7992	0.0734	10.896	0
Scaling test C	-0.283	0.1207	-2.3443	0
Joint scaling test Regression Model:	mean ~ m + a + d + aa + dd			
Regression Coefficients:				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	3.8541	0.4667	8.258	0.0767
[a]	-0.1303	0.1152	-1.1306	0.461
[d]	3.1392	1.2333	2.5453	0.2383
[aa]	0.7858	0.4096	1.9186	0.3059
[dd]	-2.0952	0.8606	-2.4346	0.2481
Residual Standard Error	10.5384			
Multiple R-square	0.9999			
Adjusted R-square	0.9994			
F-value	2166.91			
p-value	0.0163			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	4.693987	4.509646		
P_2	4.56969	4.770184		
F_1	4.898117	4.898117		
F_2	4.899927	4.899927		
$BC_{1.1}$	4.9991	5.031237		
$BC_{1.2}$	5.198366	5.161506		
Chi-square value:	111.0572			
p-value:	5.75E-26			

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action

produce favorable results when done thoroughly in later segregating generations and by using selection methods such as recurrent selection, as the inheritance of these yield and yield-associated traits were complex and polygenic. Plant maturity, days to 50% emergence, and biomass weight were found to be quantitatively inherited.

Table 3 g: Generation Mean Analysis of Days to maturity

MATURITY (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	0.4774	0.0026	53.3943	0
Scaling test B	0.4744	0.0039	122.0534	0
Scaling test C	0.0125	0.0323	0.388	0.6984
Joint scaling test Regression Model:	mean ~ m + a + d + aa + dd			
Regression Coefficients:				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	8.9881	0.1548	58.0805	0.011
[a]	0.1241	0.0371	3.3448	0.1849
[d]	1.2266	0.4054	3.0253	0.2032
[aa]	0.533	0.1443	3.6928	0.1684
[dd]	-0.6753	0.2798	-2.4138	0.25
Residual Standard Error	6.8637			
Multiple R-square	1			
Adjusted R-square	1			
F-value	66741.0238			
p-value	0.0029			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	9.601948	9.645073		
P_2	9.436505	9.39695		
F_1	9.539289	9.539289		
F_2	9.432502	9.432502		
$BC_{1.1}$	9.641785	9.627772		
$BC_{1.2}$	9.484445	9.503711		
Chi-square value:	47.11025			
p-value:	6.71E-12			

Where; m: Mid-parent value, a: Net additive gene action, d: Net dominance gene action, aa: net additive x additive gene action, ad: net additive x dominance gene action, dd: net dominance x dominance gene action.

Table 3 g Contd: Generation Mean Analysis of Days to maturity

MATURITY (WW)				
	Estimate	**SE**	**T-test**	**P-value**
Scaling test A	0.1423	0.0175	8.1146	0
Scaling test B	-0.0069	0.0182	-0.3802	0.7043
Scaling test C	-0.387	0.0287	-13.4774	0
Joint scaling test Regression Model:	mean ~ m + a + d + aa + dd			
Regression Coefficients:				
	Estimate	**Std. Error**	**t-value**	**Pr(>|t|)**
M	80.5427	2.9607	27.2044	0.0234
[a]	2.3675	0.7127	3.322	0.1861
[d]	23.272	7.7756	2.9929	0.2053
[aa]	10.1317	2.7594	3.6718	0.1693
[dd]	-12.8147	5.3737	-2.3847	0.2528
Residual Standard Error	6.9111			
Multiple R-square	1			
Adjusted R-square	0.9999			
F-value	16452.62			
p-value	0.0059			
Observed and Predicted Values of Generation Means				
Generation	Observed	Predicted		
P_1	92.2	93.04182		
P_2	89.05	88.30683		
F_1	91	91		
F_2	88.975	88.975		
$BC_{1.1}$	92.9667	92.69166		
$BC_{1.2}$	89.9583	90.32417		
Chi-square value:	47.76374			
p-value:	4.81E-12			

The estimated mean effects (m), which represent the contribution due to overall mean plus the locus effects and interaction of the fixed loci, were found to be positive and highly significant for days to plant maturity for both well-watered (WW) and water-stressed (WS) environmental conditions, as well as for dry biomass yield (under WS condition). It is possible that dominance gene effects were a major factor in regulating the genetic variation of most of the studied traits (yield-associated traits) because they were several times larger than additive gene effects for the number of pods per plot, number of seeds per plot, days to 50% flowering, biomass yield, and days to plant maturity. These findings are consistent with those presented by Karademir and Gencer (2010) in their investigation on the genetic regulation of yield and related characteristics in Egyptian cotton.

Nonetheless, for the characteristics harvest index and days to 50% emergence, additive gene effects were significant and greater in magnitude than dominant gene effects, indicating the critical role additive genes play in the inheritance of these traits. According to Jagtap (1986), selection in the early segregating generations may be successful when additive effects outweigh non-additive gene activities. In the event that the non-additive component outweighs the additive impact, further generational selection will be necessary to further refine the characters. The findings of Ekinci & Başbağ (2015) and Murtaza (2005) in their investigations on the genetic regulation of yield and yield components in cotton cultivars are consistent with these results.

Based on the current study's findings, the directions in which the gene effect affected the population mean are shown by the signs associated with the estimates of the additive x additive [i], additive x dominance (j), and dominance x dominance [l] types of epistasis. The sign also revealed information on the association or dispersion of genes in the parents for additive x additive [i] and additive x dominance [j] gene interactions (Mather and Jinks, 1982).

A negative value for any of the two parameters—additive x dominant [j] or additive x additive [i]—indicates that there is a relationship between the increasing and decreasing alleles, indicating some degree of genetic dispersion in the parents.

Kabia et al. (2017) suggested that the predicted additive effect would be minor if the genes were dispersed, referencing Mather and Jinks (1982). This shows that, for that specific genotype, the trait's alleles are diminishing. of the event that the genes are associated, a large projected additive impact would result, indicating a possible increase of trait alleles in that particular genotype. If either of these two factors shows a negative or positive sign, it should be able to raise the respective trait levels even further.

In certain instances, negative values were noted for either main effects (harvest index, days to 50% emergence and flowering for WW, WS) or non-allelic interactions (addition x additive [i], dominance x dominance (j) [j], and dominance x dominance [l]). These could suggest that the alleles governing less valuable traits either dominated or controlled the alleles governing valuable traits. But the impacts of dominant and additive genes were found to work in the other way, with indications that were distinct from one another. Days to 50% emergence, days to 50% flowering, harvest index, and characteristics all showed this to be the case.

The traits under study included number of pods per plot, biomass yield, days to 50% plant emergence, days to 50% flowering, and days to maturity. It was also observed that the dominance [d] and dominance x dominance [l] gene effects were opposite for these traits, indicating a duplicate type of non-allelic interaction (epistasis) in these traits. These findings are consistent with those published by Li et al. (2018) and Ma et al. (2019), who found similar types of epistasis between yield and characteristics linked to yield in cotton. It should be noted that when epistatic effects are significant for a trait, it may be possible to break undesirable linkage in early segregations and obtain desirable segregates. For this reason, it is suggested that recurrent selection be used to handle the aforementioned crosses in the current study in order to achieve rapid improvement. Others authors, such as Giri et al. (2020) and Begna (2021), reached comparable findings.

There was non-additive gene action in the present investigation, as evidenced by narrow-sense heritability estimates that were generally lower than the comparable broad-sense heritabilities. The complex inheritance is suggested by the poor heritability estimates, which varied from 7% to 96%. The low narrow-sense heritability estimates further suggest that environmental variation mostly controls the phenotypic effect. Because of this, choosing the optimal genotype should focus more on yield components than on yield itself, especially if yield has a low narrow-sense heritability.

The variance components' heritability estimate for narrow-sense heritability was high for characteristics including seed weight, days to 50% emergence, biomass weights (fresh and dry), seed yield, and SCMR 80 DAP. This often indicates that additive gene activity governed or controlled these features, so when appropriate, heterosis breeding would be helpful in increasing these traits in groundnuts. Results from groundnut genetic analysis and gene influences of yield and yield components obtained by Songsri et al. (2008) and Girdthai et al. (2012) are positively correlated with findings in this study.

When Jayalakshmi et al. (2001) examined the heritability of F1 and F2 segregating groundnut populations, they discovered extremely high values of heritability in those populations. While the harvest index and pod yield showed low estimates of narrow-sense heritability, they reported relatively high broad-sense heritabilities (however this is typical). Consequently, in a

Table 4: Generation mean performance for growth parameters of parents and their progenies for population 1 (WW).

Generations 1	Source	Growth Habit	Days to 50% Emergence	Days to 50% Flowering	Plant Height at Flowering (cm)	Plant Height at Harvesting (cm)	Days to Maturity
P_1: Chinese (M)	Landrace Ghana	Erect/Bunch	6	21	10.3	53.3	87
P_2: Ndogba (F)	Landrace Ghana	Semi-Erect/Bunch	7	22	19.6	32.0	89
F_1: Chinese/Ndogba	Cross	Erect/Bunch	7	24	19.0	46.7	90
F_2: Chinese/Ndogba	Cross	Erect/Bunch	7	24	19.0	36.3	89
$BC_{1.1}$: Chinese/Ndogba/Chinese	Cross	Erect/Bunch	7	25	15.6	58.7	94
$BC_{1.2}$: Chinese/Ndogba/Ndogba	Cross	Erect/Bunch	6	27	10.6	49.0	93
Mean	-	-	6.7	23.8	15.6	46.0	90.3

groundnut breeding program, selection for increase of pod production and harvest index features may be helpful (Girdthai et al., 2012). On the other hand, narrow-sense heritability refers to the heredity that a plant breeder finds valuable for breeding (Girdthai et al., 2012).

Components of variation (Heritability) for different groundnut traits (using F2 and BC populations) generation mean performance for growth parameters

Table 4 presents the performance of groundnut generations under well-watered conditions. The Chinese parent (P1), characterized by an erect/bunch growth habit, emerged the quickest in 6 days and reached 50% flowering in 21 days, with an average plant height of 10.3 cm at flowering and 53.3 cm at harvest, maturing in 87 days. In contrast, the Ndogba parent (P2), a semi-erect/bunch variety, took 7 days to emerge and 22 days to flower, with a height of 19.6 cm at flowering and 32.0 cm at harvest, maturing in 89 days.

The F1 generation exhibited intermediate traits with a flowering time of 24 days, a height of 19.0 cm at flowering and 46.7 cm at harvest, and maturing in 90 days. The F2 generation showed similar flowering time and height at flowering but had a reduced harvest height of 36.3 cm and a maturity period of 89 days. Among the backcrosses, BC1.1 (Chinese/Ndogba/Chinese) outperformed with a 7-day emergence, 25-day flowering period, a height of 15.6 cm at flowering, 58.7 cm at harvest, and a maturity of 94 days. BC1.2 (Chinese/Ndogba/Ndogba) had the fastest emergence at 6 days but a longer flowering time of 27 days, reaching 10.6 cm at flowering and 49.0 cm at harvest, with a maturity of 93 days. Overall, BC1.1 demonstrated superior performance in terms of height at harvest and days to maturity under WW conditions.

Tables 5, 6 and 7 show the performance under water-stressed conditions. The Chinese parent (P1) emerged in 8 days, flowered in 25 days, and had a height of 21.5 cm at flowering and 57.3 cm at harvest, maturing in 92 days. The Ndogba parent (P2) had quicker emergence (7 days) and earlier flowering (22 days), with a height of 18.8 cm at flowering and 42.0 cm at harvest, maturing in 89 days. The F1 generation's performance was similar to its WW condition metrics, with 26 days to flower, 46.7 cm height at harvest, and a maturity period of 91 days. The F2 generation took 8 days to emerge, 24 days to flower, with a height of 21.2 cm at flowering and a significantly reduced height at harvest of 31.3 cm, maturing in 89 days.

Among the backcrosses, BC1.1 showed strong performance with 7 days to emergence, 25 days to flower, 20.6 cm height at flowering, 56.7 cm at harvest, and a maturity of 93 days. BC1.2 emerged in 7 days, flowered in 28 days, had a height of 17.6 cm at flowering and 47.0 cm at harvest, maturing in 90 days. BC1.1 again exhibited the best overall performance under WS conditions, particularly for height at harvest and days to maturity. The data highlight that BC1.1 (Chinese/Ndogba/Chinese) consistently performed best under both WW and WS conditions, indicating its strong genetic potential for drought tolerance and yield stability. This aligns with research by Rao et al. (2012), Gowda et al. (2013), and Morales et al. (2020a), who emphasized the importance of both additive and non-additive genetic factors in trait inheritance across varying environmental conditions. Such insights underscore the potential for breeding programs to enhance drought tolerance and yield stability in groundnuts, consistent with objectives outlined by Kabir et al. (2023).

Research by Upadhyaya et al. (2011) and Kakeeto et al. (2020) supports the idea that selecting high-performing parents under stress conditions can significantly improve progeny traits. Similarly, Anjum et al. (2011) and Morales et al. (2020a) highlight that drought tolerance is influenced by multiple factors, including growth habits and physiological resilience. The robust performance of BC1.1 under both conditions suggests a beneficial genetic combination from both parent lines, validating multi-approach strategies for crop improvement under stress. The significant dominance effects observed in this study are in line with findings by Gowda et al. (2013) and Upadhyaya et al. (2011), which emphasize the role of both additive and non-additive effects in drought tolerance traits. The increase in days to emergence and maturity under water-stressed conditions corroborates Rao et al. (2012), who noted similar responses to drought stress in legumes.

The complexity of genetic control involving both additive and non-additive variances is well-documented

Table 5: Generation mean performance for growth parameters of parents and their progenies for population 1 (WS).

Generations 1	Source	Growth Habit	Days to 50% Emergence	Days to 50% Flowering	Plant Height at Flowering (cm)	Plant Height at Harvesting (cm)	Days to Maturity
P_1: Chinese (M)	Landrace, Ghana	Erect/Bunch	8	25	21.5	57.3	92
P_2: Ndogba (F)	Landrace, Ghana	Semi-Erect/Bunch	7	22	18.8	42.0	89
F_1: Chinese/Ndogba	Cross	Erect/Bunch	7	26	19.0	46.7	91
F_2: Chinese/Ndogba	Cross	Erect/Bunch	8	24	21.2	31.3	89
$BC_{1.1}$: Chinese/Ndogba/Chinese	Cross	Erect/Bunch	7	25	20.6	56.7	93
$BC_{1.2}$: Chinese/Ndogba/Ndogba	Cross	Erect/Bunch	7	28	17.6	47.0	90
Mean	-	-	7.3	25.0	19.8	46.8	92.7

Table 6: Generation Mean performance for growth parameters of parents and their progenies for population 2 (WW).

Generations 2	Source	Growth Habit	Days to 50% Emergence	Days to 50% Flowering	Plant Height at Flowering (cm)	Plant Height at Harvesting (cm)	Days to Maturity
P_1: Sinkara (M)	Landrace, Ghana	Erect/Bunch	8	27	11.0	47.7	89
P_2: Chaco-pag (F)	Landrace, Ghana	Erect/Bunch	7	25	16.6	50.7	90
F_1: Sinkara/Chacopag	Cross	Erect/Bunch	7	28	10.3	40.7	90
F_2: Sinkara/Chaco-pag	Cross	Erect/Bunch	8	28	9.0	44.0	90
$BC_{1.1}$: Sinkara/Chacopag/Sinkara	Cross	Erect/Bunch	6	27	10.6	49.0	93
$BC_{1.2}$: Sinkara/Chacopag/Chaco-pag	Cross	Erect/Bunch	8	29	15.13	48.7	92
Mean	-	-	7.3	27.3	12.1	46.8	90.7

Table 7: Generation mean performance for growth parameters of parents and their progenies for population 2 (WS).

Generations 2	Source	Days to 50% Emergence	Days to 50% Flowering	Plant Height at Flowering (cm)	Plant Height at Harvesting (cm)	Days to Maturity
P_1: Sinkara (M)	Landrace, Ghana	9	29	16.8	57.2	93
P_2: Chaco-pag (F)	Landrace, Ghana	7	25	11.6	55.7	89
F_1: Sinkara/Chacopag	Cross	7	26	10.3	37.9	90
F_2: Sinkara/Chacopag	Cross	8	28	8.9	48.0	89
$BC_{1.1}$:Sinkara/Chacopag/Sinkara	Cross	9	29	10.6	52.6	92
$BC_{1.2}$:Sinkara/Chacopag/Chaco-pag	Cross	7	24	16.1	47.7	94
Mean	-	7.8	26.8	12.4	48.2	91.2

in crop studies. Ali *et al.* (2011) found that both types of variances are crucial in maize under drought conditions, a finding echoed in this study. The observed phenotypic stability in days to 50% flowering and maturity under both conditions indicates that some genotypes possess inherent resilience to drought, a desirable trait for breeding programs aimed at improving drought tolerance (Cattivelli et al., 2008).

Generation mean performance for growth parameters of parents and their progenies for population

Under WW conditions, P1 (Sinkara) and P2 (Chaco-pag), both landraces from Ghana, exhibited an erect/bunch growth habit (Tables 4 and 5). P2 (Chaco-pag) outperformed P1 (Sinkara) with earlier emergence (7 days vs. 8 days) and higher average plant height at flowering (16.6 cm vs. 11.0 cm) and harvesting (50.7 cm vs. 47.7 cm). The F1 generation showed slightly delayed flowering (28 days) compared to the parents but maintained similar maturity times (90 days). Among the backcrosses, BC1.2 (Sinkara/Chaco-pag/Chaco-pag) achieved the highest average plant height at flowering (15.13 cm), indicating superior growth under optimal water conditions.

Under WS conditions, P2 (Chaco-pag) again emerged and flowered earlier (7 days and 25 days, respectively) compared to P1 (Sinkara), which took 9 days to emerge and 29 days to flower (Tables 6 and 7). However, P1 exhibited greater average plant height at flowering (16.8 cm vs. 11.6 cm) and at harvesting (57.2 cm vs. 55.7 cm). The F1 and F2 generations displayed reduced plant height under WS conditions, with F2 showing the lowest height at flowering (8.9 cm) and at harvesting (48.0 cm). BC1.2 (Sinkara/Chaco-pag/Chaco-pag) demonstrated the best performance with early flowering (24 days), greater height at flowering (16.1 cm), and good height at harvest (47.7 cm), indicating better drought tolerance. BC1.2 consistently performed well under both conditions, showcasing the highest average plant height at flowering under WW conditions and early flowering with good height under WS conditions. This suggests that BC1.2 may possess favorable genetic traits for both optimal and stressed environments, making it a promising candidate for breeding drought-tolerant groundnuts.

Previous research supports these findings, noting that backcross generations often show improved traits due to favorable alleles from both parents. Studies by Upadhyaya et al. (2011) and Kakeeto et al. (2020) emphasize the effectiveness of backcross breeding in enhancing drought tolerance, aligning with the observed performance of BC1.2 in this study.

Mean performance for growth parameters of parents and their progenies for populations 1 and 2 under well-watered (WW) and water-stressed (WS) conditions

The groundnut populations in this study demonstrated similar growth patterns under well-watered (WW) and water-stressed (WS) conditions. For Population 1, emergence occurred in seven days, with flowering at 24 days under WW and 25 days under WS. Heights at flowering (16 cm WW, 20 cm WS) and harvest (46 cm WW, 47 cm WS) were similar, indicating that water stress slightly increased early growth but had minimal effect on final height. Maturity was delayed by three days under WS (90 days WW, 93 days WS), consistent with Jaleel et al. (2009), who noted that water stress can extend the vegetative period.

Population 2 showed no significant differences in emergence and flowering times between WW and WS conditions. Heights at flowering (12 cm WW, 12 cm WS) and harvest (47 cm WW, 48 cm WS) were nearly identical, with maturity achieved in 91 days for both conditions. This uniformity in growth habit aligns with Songsri et al. (2008), who observed that growth habit can be steady despite environmental stress. These findings highlight the resilience of groundnut plants to water stress, maintaining growth rates and phenological milestones. The minimal differences suggest genetic stability in groundnuts, making them promising candidates for drought-resistant breeding programmes.

Conclusion

The study investigated the genetic control of drought tolerance and yield-associated traits in groundnut using generation mean and variance analysis. Both additive and dominance gene effects significantly influenced traits like pod yield, seed yield, biomass yield, and days to maturity. All three gene actions- additive x additive, additive x dominance, and dominance x dominance—were present. High narrow and broad sense heritabilities for seed weight, yield, and biomass, along with their positive correlation with pod yield, indicate these traits are good for yield selection in improvement programs. Moderate heritability for days to maturity, strongly correlated with days to emergence and flowering, supports its use for selecting earliness. Dominance gene effects were crucial for yield variance and earliness, while additive effects predominated in economic yield traits. The research highlights the complex genetic regulation of drought tolerance, emphasizing the importance of both additive and non-additive gene activities. Future work should identify genetic markers to enhance marker-assisted selection for stress-resilient, high-yielding groundnut varieties.

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