DOI: https://dx.doi.org/10.4314/gjass.v24i1.2

GLOBAL JOURNAL OF AGRICULTURAL SCIENCES VOL. 24, 2025: 7-28
COPYRIGHT© BACHUDO SCIENCE CO. LTD PRINTED IN NIGERIA ISSN 1596-2903 e-ISSN: 2992 – 4499
www.globaljournalseries.com.ng, Email: globaljournalseries@gmail.com

ESTIMATING THE INHERITANCE OF DROUGHT-TOLERANCE AND YIELD-ASSOCIATED TRAITS OF GROUNDNUT (*Arachis hypogaea* L.) USING GENERATION MEAN AND VARIANCE ANALYSIS OF PARENTAL, F_1 AND THE SEGREGATING POPULATIONS (backcrosses and F_2)

OPPONG-SEKYERE, DANIEL, ADUGUBA, ORLANDO WILBERFORCE AND ESSEL, JOHN HENDERICK
E-mail: oaduguba@bolgatu.edu.gh

(Received 13 January 2025; Revision Accepted 20 January 2025)

ABSTRACT

Groundnut (Arachis hypogaea L.) is a vital legume crop globally, particularly in semi-arid regions where drought stress significantly hampers yield and productivity. The inheritance of drought tolerance and yield-associated traits remains a key challenge in groundnut breeding programs. This study aims to estimate the genetic basis of drought tolerance and yield-associated traits using generation mean and variance analysis of parental, F1, and segregating populations (F2 and backcrosses). The study was conducted at the Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, Ghana. Hybridization activities were carried out in a screen house starting on August 2, 2022, to develop bi-parental crosses. Field evaluations of parental lines (P1 and P2), F1, F2, and backcross generations (BC1.1 and BC1.2) were conducted between January and November 2023 under two water regimes: well-watered (WW) and water-stressed (WS) conditions. The experimental design was a randomized complete block design (RCBD) with four replications. The genetic material included the drought-tolerant landrace Chinese (M) and three other landraces, Sinkara (M), Ndogba (F), and Chaco-pag (F), selected for their high pod, seed, and biomass yields, as well as their farmer-preferred traits. Analysis of variance revealed significant differences among generations for traits such as days to flowering, plant height, pod weight, seed weight, and biomass yield. Estimates of narrow-sense heritability (h2n) ranged from 0.07 (harvest index) to 0.96 (dry biomass), while broad-sense heritability (H2b) values were consistently high (>0.65), indicating strong genetic influence on these traits. Generation mean analysis suggested the predominance of additive gene action for most traits, though dominance and epistatic interactions were also significant for specific traits.

KEYWORDS: Arachis hypogaea L.; Early-maturing; Drought-tolerant; heritability; additive

INTRODUCTION

Globally, groundnuts (*Arachis hypogaea* L.) are prized for their easily digestible protein and superior edible oil. With an average yield of 1.5 tons ha-1, it is grown on 23.4 million hectares and produces 34.9 million metric tons yearly (Grandawa, 2014). Around two-thirds of the world's groundnut production, which is produced in 108 nations, comes from rainfed tropical, subtropical, and warm regions (Rao et al., 2012). Compared to areas where it is grown commercially, productivity in these rainfed areas is substantially lower (Gowda et al., 2013). Drought resistance is a primary breeding goal in groundnut enhancement efforts since it is a major factor limiting yield.

It is important to create drought-resistant, high-yielding, early-maturing groundnut varieties for areas like Northern Ghana, the Upper East, and the Upper West of Ghana, where rainfall is essential to agriculture and droughts negatively affect output.

Oppong-Sekyere, Daniel, Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, P. O. Box 767, Bolgatanga, Upper East Region, Ghana

Aduguba, Orlando Wilberforce, Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, P. O. Box 767, Bolgatanga, Upper East Region, Ghana

And Essel, John Henderick, Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, P. O. Box 767, Bolgatanga, Upper East Region, Ghana

In these regions, end-of-season drought is common, and production can be increased by breeding for drought resistance (Fita et al., 2015; Raza et al., 2023). Using multi-approach ways to increase crop development under conditions of climate change, current research endeavors to comprehend the physiological, morphological, and biochemical mechanisms of drought tolerance in crops such as sorghum and groundnuts (Anjum et al., 2011; Morales et al., 2020). Due to its effects on the ozone layer and decrease in soil moisture, climate change brought on by human activity makes drought worse (Kabir et al., 2023). When phenotyping crops such as sorghum for drought tolerance, characteristics such as disease resistance, nutrient shortage, and plant age are taken into account (Mwamahonje et al., 2021). In groundnut breeding, drought-resistant variants require selection based on attributes like transpiration efficiency (TE), specific leaf area (SLA), and Soil-Plant Analytical Development (SPAD) Chlorophyll Meter Readings (SCMR) (Nigam and Aruna, 2008; Oppong-Sekyere et al., 2019). According to Richardson et al. (2002) and Sheshshayee et al. (2006), SCMR is a dependable, non-invasive substitute for TE that offers information on the light-transmittance characteristics of the leaf based on its chlorophyll concentration. Studies on groundnut for SLA and SCMR have revealed substantial genetic variation, and TE and SCMR have been found to positively correlate (Bindu Madhava et al., 2003; Sheshshayee et al., 2006).

When phenotyping crops such as sorghum for drought tolerance, characteristics such as disease resistance, nutrient shortage, and plant age are taken into account (Mwamahonje et al., 2021). In groundnut breeding, drought-resistant variants require selection based on attributes like transpiration efficiency (TE), specific leaf area (SLA), and Soil-Plant Analytical Development (SPAD) Chlorophyll Meter Readings (SCMR) (Nigam and Aruna, 2008; Oppong-Sekyere et al., 2019). According to Richardson et al. (2002) and Sheshshayee et al. (2006), SCMR is a dependable, non-invasive substitute for TE that offers information on the light-transmittance characteristics of the leaf based on its chlorophyll concentration. Studies on groundnut for SLA and SCMR have revealed substantial genetic variation, and TE and SCMR have been found to positively correlate (Bindu Madhava et al., 2003; Sheshshayee et al., 2006). The success of selection based on additive genetic variance depends on heritability, or the fraction of phenotypic variance attributable to genetic variation (Mulder et al., 2016; Oppong-Sekyere et al., 2019). This study combines generation mean and variance analysis of parental, F1, and segregating populations (backcrosses and F2) to assess the inheritance 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, 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 (4) replications. Plot sizes adopted were 5 m by 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.

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 conditions (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 (3) 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 %, and drought tolerant and farmer-preferred.

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 1). The male parents (Chinese and Sinkara) constituted the parents that were drough 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_1s generated (Chinese x Ndogba) were also backcrossed to the susceptible female parent (Ndogba) to produce $BC_{1.2}$ population. Some of the F_1s (Chinese x Ndogba) produced in the first parental cross were advanced, through selfing, to generate F_2 segregating population (Figure 1).

For population two, 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. The F_1 was again backcrossed to the drought susceptible female parent (Chaco-pag) to produce $BC_{1.2.}$ Some of the F_1s for population two (Sinkara x Chaco-pag) were advanced by selfing them to produce F_2 segregating population (Figure 2). About eight (8) crosses were made on each individual female to increase hybrid seeds. At harvest, all F_1 plants were examined carefully for several morphological traits including plant height, leaf color, pod and seed characters and compared with both parents to confirm their hybridity.

The F_1 crosses were harvested during the first week of December, 2022. Harvesting of F_2s was done in September, 2023. Seeds of F_1s, F_2s, parents 1 and 2 and $BC_{1.1}$ and $BC_{1.2}$ for the two populations were saved for subsequent genetic studies.

Crossing Block Layout for Hybridization Activities

Table 1: Crossing block layout

Females	**Males**
Ndogba	Chinese
Chaco-pag	Sinkara

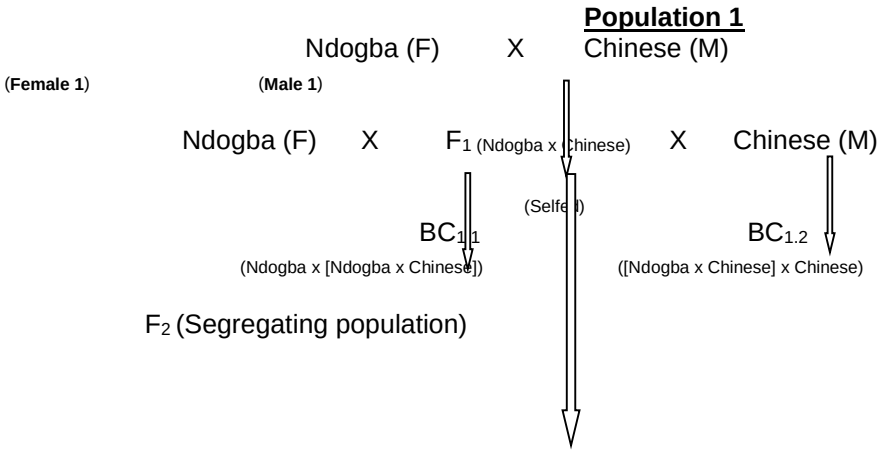

Figure 1: Design to generate the various populations for generation mean analysis (for Population 1)

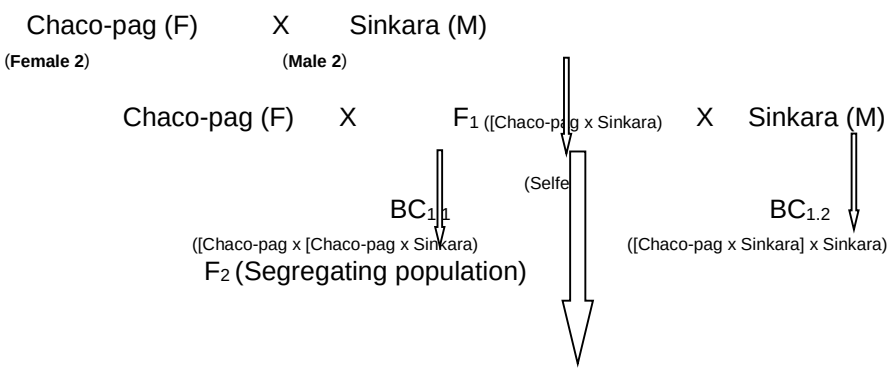

Figure 2: Design to generate the various populations for generation mean analysis (for Population 2).

Generation Mean and Variance Analysis for Groundnut Populations under Well-Watered and Water-Stressed Conditions

In the 2023 season, six generations (P1, P2, F1, F2, BC1.1, and BC1.2) of groundnut populations were planted at the experimental fields of the Department of Ecological Agriculture, School of Agriculture, Bolgatanga Technical University, Bolgatanga, Upper East, Ghana.

The experimental setup included two ridges for each parent and F1s, seven ridges for backcrosses, and twelve ridges for F2 plants to minimize inter-genotypic competition and adequately sample genetic variability. Each ridge consisted of 20 plants, spaced 20 cm apart and 60 cm wide, thinned to one plant per hill. The groundnut generations were tested under two water regimes: well-watered (WW) and water-stressed (WS) conditions. Data were collected from 20, 20, 25, 200, 120, and 120 plants from P1, P2, F1, F2, BC1.1, and BC1.2, respectively, for parameters including 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. Measurements followed procedures by Upadhyaya et al. (2011) and Kakeeto et al. (2020).

Harvest Index (HI) was estimated using the formula:

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

(Girdthai *et al*., 2010) (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)

Plants were sampled at random and the second fully expanded leaf from the top of the main stem was used for SCMR assessment during the morning period (Nageswara *et al*., 2001). The chlorophyll content was recorded on each of the four leaflets of the tetrafoliate leaf. An average SCMR for each plot was derived from 20 single observations (four leaflets x 5 plants per plot) (Arunyanark *et al*., 2008). Care was taken to ensure that the SPAD meter sensor fully covered the leaf lamina in order to avoid interference from veins and midribs during the SCMRs (Nageswara *et al*., 2001).

Drought Tolerance Index (DTI)

According to Nautiyal et al. (2002), each characteristic's value was defined as the ratio of the trait value—for example, pod yield—measured under water-stressed (WS) conditions over the value recorded under well-watered (WW) conditions. 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 (Nautiyal et al., 2002).

Statistical and Genetic Analysis

Data on traits were analyzed using ANOVA with the GenStat statistical package (Discovery Edition 6). Data for traits were subjected to Analysis of Variance (ANOVA) using GenStat statistical package (Discovery Edition 4). Standard Error of the Difference (SED) at 5% was used to determine the significant differences among the means of the various generations. Correlations among groundnut genotypes as well as mean squares of traits from ANOVA among the groundnut crosses for the two (2) water regimes were estimated.

Generation mean analysis using scaling tests A, B and C proposed by Mather (1949) and joint scaling test of Cavalli (Cavalli, 1952) were estimated by using the 'R' statistical software and the Plant Breeder's Tools statistical software to determine the genetic control of some of the yield and yield-associated traits (Harvest index, number of pods per plot, number of seeds per plot, biomass yield, days to 50% emergence, days to 50% flowering and days to maturity). The A, B and C scaling tests were calculated individually to determine the adequacy of the additive-dominance model by their significant deviation or equality to zero and by a significant chi-square (X^2) (Kabbia *et al*., 2017). The model was deemed adequate when all of each individual value is equal to zero. However, inadequacy of the additive x dominance model indicates the expression of complex genetic factors (non-allelic interaction or epistasis, linkage and multiplication effects) present in the inheritance of the trait; thus, a Cavalli's joint scaling test was done (Mather and Jinks, 1982). A log transformation was, nonetheless used to normalize the raw data for the population (Mather and Jinks, 1982; Kabbia *et al*., 2017). A corresponding standard error (SE) for each test was used as a denominator to determine the calculated t-test. Significance of the values of A, B, and C was determined by comparing the calculated and tabulated 't' values, at a degree of freedom (df) determined by summing up the individual df of each parameter (Kabbia *et al*., 2017). Test of significance (t-test) for the scaling tests A, B and C, was done by comparing calculated t-value with the table values at 5% level of significance.

Gene Interactions and Scaling Tests

Scaling tests A and B, when significant, indicate the presence of three types of non-allelic gene interactions: additive × additive (i), additive × dominance (j), and dominance × dominance (l).

A significant scaling test C suggests the dominance × dominance (l) interaction (Singh & Narayanan, 1993; Kabbia et al., 2017).

Scaling Test Formulae

Cavalli's joint scaling test evaluates goodness-of-fit in a single step, identifying the source of misfit if present (Kabbia et al., 2017).

Generation means are influenced by three parameters: mid-parent value (m), additive effects ([d]), and dominance effects ([h]). These were estimated using a generalized inverse matrix equation ($M = J^{-1}S$), where weights are reciprocals of generation mean variances (1/Vx). Chi-square (X^2) tests compared observed vs. expected values (Singh & Narayanan, 1993; Kabbia et al., 2017).

Interpretation of Scaling Tests (A, B, and C)

If $p > 0.05$, the additive-dominance model sufficiently explains genetic variation, suggesting no significant maternal or epistatic effects. If $p < 0.05$, the model is inadequate, requiring further regression analysis (Kearsey & Pooni, 1996).

Heritability Estimation

Heritability was estimated using the variance component method via ANOVA for a bi-parental mating design. The total variance (VP) was partitioned as:

VP = VG + VE + VGE,

where VG includes additive (VA), dominance (VD), and interaction variance (VI). Additive variance (VA) primarily determines genetic inheritance and response to selection.

Heritability estimate using basic generations

Heritability estimation in groundnut populations was derived from variance components of six generations, including parental, F1, F2, and backcross progenies. The total phenotypic variance (V_P) was partitioned into additive (V_A), dominance (V_D), and environmental (V_E) variances. The variance components were defined as follows:

V_{P1} and V_{P2} represent the variances of Parent 1 and Parent 2.

V_{F1} and V_{F2} denote the variances of F1 and F2 progenies.

$V_{BC1.1}$and $V_{BC1.2\ are}$ the variances of backcross progenies to Parent 1 and Parent 2, respectively.

Using these variances, the additive and dominance components were estimated with the formulas:

$V_A = 2V_{F2} - (V_{BC1.1} + V_{BC1.2})$

$VD = (V_{BC1.1} + V_{BC1.2}) - V_{F2} - V_{EV}$

Heritability estimates were classified into broad-sense (H^2) and narrow-sense (h^2) heritability.

1. **Broad-sense heritability**, which accounts for total genetic variance, was calculated as:

$$H^2 = V_G V_P$$

2. **Narrow-sense heritability**, which focuses on additive genetic variance and is more relevant for selection in breeding, was computed as:

$$h^2 = \frac{VA}{VP}$$

RESULTS AND DISCUSSION

Heritability estimates for pod, seed traits, flowering, maturity, and growth parameters.

Heritability Estimates: Both broad- and narrow-sense heritability (H^2) and h^2 provide information about the genetic makeup of groundnut attributes. The h^2 estimates in this investigation varied from 7% to 96%. Strong additive genetic control is indicated by high h^2 for characteristics such as dry biomass weight (96%) and number of seeds per plot (89%), which is consistent with earlier research by Fonceka et al. (2012) and Pandey et al. (2014). These high estimates imply that these features would be a useful basis for selection. On the other hand, characteristics such as the harvest index and the quantity of pods per plot demonstrated high H^2 (78% and 98%) but low h^2 (7% and 12%, respectively), suggesting significant non-additive genetic variance. This is consistent with the findings of Nigam et al. (2001), who also observed low h^2 but high H^2 in groundnut yield traits, suggesting the influence of dominance and epistasis.

Pod and Seed Numbers: Significant variations were found in the scaling test findings for the number of pods and seeds per plot, suggesting that the additive-dominance model was unable to adequately explain variation in both well-watered (WW) and water-stressed (WS) situations. Complex genetic control is suggested by the existence of non-allelic interactions such as dominance x dominance, additive x additive, and additive x additive. These results are consistent with those of Upadhyaya et al. (2001), who also found substantial epistatic interactions in the yield attributes of groundnuts. Under both circumstances, the net additive effects were greater than the net dominance effects, indicating that additive genetic variance is important for these traits.

Plant Emergence and Flowering: Mather's scaling test showed significant non-allelic gene interactions under WW conditions, but not under WS conditions, for days to 50% plant emergence. The findings of Hamidou et al. (2012), who also discovered over-dominance in groundnut characteristics under stress conditions, are supported by the negative values for the net additive x additive and net dominance effects, which imply that alleles favoring early emergence are recessive. Days to 50% flowering similarly revealed substantial non-allelic interactions under both circumstances, and there was over-dominance for early flowering features as well as negative net additive and net dominance x dominance effects.

Days to Maturity: Significant non-allelic interactions were also shown by days to maturity, with more intense net dominance effects than net additive effects in both scenarios. According to this, dominance interactions have a major impact on the maturity period, which is in line with the findings of Holbrook et al. (2009), who highlighted the significance of dominance in groundnut maturation features.

The quantitative inheritance indicated by the positive and substantial mid-parent values provides more evidence for the intricate genetic regulation of this feature.

Growth Parameters under Different Conditions: In comparison to WS conditions, groundnuts in WW conditions generally performed better in terms of emergence and flowering periods, plant height, and days to maturity, according to the mean performance for growth metrics. This is in line with earlier research (Bhatnagar-Mathur et al., 2007; Xue et al., 2018) that emphasizes the effect of water availability on plant growth and development. The resilience of these features to environmental stress is highlighted by the minor differences in height and maturity between populations 1 and 2 under various water circumstances, which is essential for developing drought-tolerant cultivars.

Table 2: Variation (Heritability) for different groundnut traits based on 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% to 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.

Generations under Well-Watered (WW) and Water-Stressed (WS) Conditions

Harvest Index: The scaling tests A, B, and C, based on Mather (1949), revealed no significant difference from zero ($P \geq 0.05$) for harvest index (HI) under both well-watered (WW) and water-stressed (WS) conditions for groundnut generations (Table 3a). The joint scaling test indicated that the additive-dominance model alone adequately explained the variation among the harvest indices (Table 3a). The HI demonstrated a mid-parent value of 0.519 (WW) and 0.49 (WS), with a net additive score of 0.16 (WW) and 0.17 (WS). A negative net dominance effect of -0.077 (WW) and -0.015 (WS) was observed, indicating some level of gene dispersion in the parents, resulting in a small estimated additive effect. This suggests that the alleles responsible for HI in groundnut genotypes are decreasing (Table 3a). This pattern of gene interaction, where alleles controlling low-value traits dominate, has been noted in other studies, such as those by Akande et al. (2014), which discuss the implications of gene dispersion on breeding programs focused on increasing yield traits.

Seed and Pod Number: The scaling test results for the number of seeds per plot under well-watered (WW) conditions indicated significant differences, suggesting that the additive-dominance model alone is inadequate. Non-allelic gene interactions, including additive x additive, additive x dominance, and dominance x dominance, complicate the genetic inheritance of seed yield under these conditions. In water-stressed (WS) environments, the results indicated a predominant additive x dominance gene effect, with net dominance effects larger than additive effects, highlighting gene dispersion and interactions between decreasing alleles (Table 5b). For pod number, scaling tests under WW conditions showed similar significant differences, indicating non-allelic gene interactions like those observed for seed number. Under WS conditions, significant differences in scaling test A suggested complex gene interactions, with dominance x dominance gene action being prominent.

This complexity in genetic control is consistent with findings from Upadhyaya et al. (2011), who reported significant heritability estimates for pod and seed yield in groundnuts under drought conditions. Similarly, Gautami et al. (2012) found that both additive and non-additive genetic effects are crucial in the inheritance of drought-tolerance traits. These studies emphasize the importance of considering the intricate genetic architecture in breeding programs to enhance drought tolerance and yield in groundnuts.

Biomass Yield: All three scaling tests (A, B, and C) for biomass yield (both fresh and dry) showed significant differences from zero ($p < 0.05$) for both well-watered (WW) and water-stressed (WS) environments, indicating that the additive-dominance model alone is insufficient (Table 3d). This suggests the presence of non-allelic gene interactions, including additive x additive, additive x dominance, and dominance x dominance, in the groundnut crosses under both water conditions. The joint scaling test for dry biomass yield under WW revealed a negative net dominance x dominance effect (-0.83), suggesting gene dispersion with a small additive effect (0.08). A similar trend was observed under WS, though the net dominance x dominance effect was positive (0.019). These results suggest that decreasing alleles for biomass yield are present in the genotype (Table 5d). Net dominance effects were larger than net additive effects under both water regimes, highlighting the complexity of the genetic control of biomass yield. These findings align with previous research by Vadez et al. (2013), which discussed the role of both additive and non-additive genetic effects in biomass accumulation under stress conditions. Another study by Nageswara Rao et al. (2014) emphasized the importance of gene interactions in determining biomass yield, particularly under drought conditions. These results underscore the need to consider complex gene interactions in breeding programs aimed at improving biomass yield in groundnuts

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	
p-value:	0.477836	

HARVEST INDEX (WS)

	Estimate	SE	T-test	Pvalue
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	

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 b: Generation Mean Analysis of Number of Pods per Plot

POD NUMBER (WW)

	Estimate	SE	T_test	Pvalue
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

RegressionCoefficients:

	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	

POD NUMBER (WS)

	Estimate	SE	T_test	Pvalue
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

RegressionCoefficients:

	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

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

SEED NUMBER (WW)

	Estimate	SE	T_test	Pvalue
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

RegressionCoefficients:

	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	

SEED NUMBER (WS)

	Estimate	SE	T_test	Pvalue
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 StandardError	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

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

BIOMASS (DRY) (WS)

	Estimate	SE	T-test	P-value
Scaling test A	0.1722	5.00E-04	345.7247	0
Scaling test B	0.0071	7.00E-04	10.812	0
Scaling test C	-0.4135	9.00E-04	-443.027	0

JOINT SCALING TEST

Regression Model: mean ~ m + a + d + aa + dd

RegressionCoefficients:

	Estimate	Std. Error	T-value	Pr(>|t|)
M	2.4572	0.085	28.9124	0.022
[a]	0.019	0.0856	0.2217	0.8611
[d]	0.3664	0.1244	2.9455	0.2084
[aa]	0.1239	0.1185	1.0451	0.486
[dd]	0.2581	0.2157	1.1967	0.4432

Residual Standard Error	526.0682
Multiple R-square	0.9999
Adjusted R-square	0.9996
F-value	3252.952
p-value	0.0133

Observed and Predicted Values of Generation Means

Generation	Observed	Predicted
P_1	2.622411	2.600054
P_2	2.61724	2.562115
F_1	2.837525	2.823607
F_2	2.652119	2.640413
BC1.1	2.728621	2.74539
BC1.2	2.554221	2.597369

Chi-square value:	276747.8
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

Plant Emergence: Mather's scaling test for days to 50% plant emergence revealed no significant differences ($p > 0.05$) for scaling tests A ($p = 0.8102$) and C ($p = 0.1155$), but scaling test B showed significance ($p = 0$) under the well-watered (WW) condition (Table 3e). The presence of significant differences in at least one of the scaling tests suggests that non-allelic gene interactions, including additive x additive, additive x dominance, and dominance x dominance, are at play among the groundnut crosses. Under water-stressed (WS) conditions, scaling test B was not significant ($p = 0.8977$), yet the presence of significance in other tests indicates the presence of gene interactions (Table 3e). The joint scaling test estimates showed a net dominance x dominance gene action for both WW and WS conditions, with negative signs for net additive x additive interaction (WW: -3.946, WS: -0.333) and net dominance effects (WW: -9.634, WS: -0.78), suggesting decreasing alleles for plant emergence traits (Table 3e). The negative values for non-allelic interactions indicate that alleles for lower values dominate over those for higher values.

Plant Flowering: Mather's scaling test for days to 50% flowering under well-watered (WW) conditions showed no significance ($p > 0.05$) for scaling test C ($p = 0.1155$), indicating the presence of dominance x dominance (l) non-allelic gene interaction among the groundnut crosses (Table 3f). However, the significance of scaling tests B and C under water-stressed (WS) conditions suggests the presence of all three types of gene interactions: additive x additive, additive x dominance, and dominance x dominance (Table 3f). Joint scaling test estimates for days to 50% flowering revealed negative signs for net additive effects (WW: -0.1205, WS: -0.1303) and net dominance x dominance effects (WW: -1.8118, WS: -2.0952), indicating gene dispersion and the presence of decreasing alleles for flowering traits (Table 3f). The negative values for non-allelic interactions suggest that alleles for lower value traits are over-dominant, influencing the trait expression. These findings align with previous studies, such as those by Chandra et al. (2013), which noted the significance of gene interactions in determining flowering time under varying environmental conditions. Other research by Nariani and Parimoo (2010) supports these results, emphasizing the complexity of genetic control in flowering traits, particularly under stress conditions.

Days to Maturity: Mather's scaling test for days to maturity indicated no significant difference ($p > 0.05$) for scaling test C ($p = 0.6984$) under well-watered (WW) conditions (Table 5g). However, the significance of scaling tests A and B suggests the presence of all three types of non-allelic gene interactions: additive x additive, additive x dominance, and dominance x dominance. Under water-stressed (WS) conditions, scaling test B was not significant ($p = 0.7043$), but the significance of scaling tests A and C indicates the presence of these gene interactions (Table 3g). The joint scaling test estimates revealed negative signs for net dominance x dominance gene effects under both WW (-0.6753) and WS (-12.8174) conditions, indicating gene dispersion and the presence of decreasing alleles for maturity traits (Table 3g). The net dominance effect was higher than the net additive effect under both water regimes, highlighting the complexity of genetic control for maturity traits. The mid-parent values for both WW (8.9881) and WS (80.5427) were positive and significantly different from zero, suggesting that the traits were quantitatively inherited (Table 3g). These findings are consistent with studies by Mallikarjuna et al. (2012), which discuss the role of gene interactions in determining maturity traits under varying environmental conditions. Similar results have been reported by Vishnu et al. (2011), emphasizing the importance of considering both additive and non-additive genetic effects in breeding programs aimed at improving days to maturity in groundnut.

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	

EMERGENCE (WS)

	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	2.654524	2.730915
P_2	2.441672	2.387077
F_1	2.626246	2.626246
F_2	2.630748	2.630748
$BC_{1.1}$	2.648809	2.633393
$BC_{1.2}$	2.436634	2.461474
Chi-square value:	5.7375	
p-value:	0.016606	

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 f: Generation Mean Analysis of Days to 50% flowering

FLOWERING (WW)

	Estimate	SE	T_test	Pvalue
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

RegressionCoefficients

	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	

FLOWERING (WS)

	Estimate	SE	T_test	pvalue
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

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	

MATURITY (WS)

	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
BC1.1	92.9667	92.69166
$BC_{1.2}$	89.9583	90.32417
Chi-square value:	47.76374	
p-value:	4.81E-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 4: Generation Mean Performance for Growth Parameters of Parents and their Progenies for Population 1 and 2 (WW and WS)

Generations 2	Source	Growth Habit	Days to 50% Emergence (days)	Days to 50% Flowering (days)	Avg. Plant Height @ Flowering (cm)	Avg. Plant Height @ Harvesting (cm)	Days to Maturity (days)
P1: Sinkara (M) WW	Landrace, Ghana	Erect/Bunch	8	27	11	47.7	89
P2: Chaco-pag (F) WW	Landrace, Ghana	Erect/Bunch	7	25	16.6	50.7	90
F1: Sinkara/Chaco-pag WW	Cross	Erect/Bunch	7	28	10.3	40.7	90
F2: Sinkara/Chaco-pag WW	Cross	Erect/Bunch	8	28	9	44	90
BC1.1: Sinkara/Chaco-pag/Sinkara WW	Cross	Erect/Bunch	6	27	10.6	49	93
BC1.2: Sinkara/Chaco-pag/Chaco-pag WW	Cross	Erect/Bunch	8	29	15.13	48.7	92
Mean WW	-	-	7.3	27.3	12.1	46.8	90.7
P1: Sinkara (M) WS	Landrace, Ghana	Erect/Bunch	9	29	16.8	57.2	93
P2: Chaco-pag (F) WS	Landrace, Ghana	Erect/Bunch	7	25	11.6	55.7	89
F1: Sinkara/Chaco-pag WS	Cross	Erect/Bunch	7	26	10.3	37.9	90
F2: Sinkara/Chaco-pag WS	Cross	Erect/Bunch	8	28	8.9	48	89
BC1.1: Sinkara/Chaco-pag/Sinkara WS	Cross	Erect/Bunch	9	29	10.6	52.6	92
BC1.2: Sinkara/Chaco-pag/Chaco-pag WS	Cross	Erect/Bunch	7	24	16.1	47.7	94
Mean WS	-	-	7.8	26.8	12.4	48.2	91.2

Generation Mean Analysis for Drought and Yield-Associated Traits

Understanding the genetic control of key traits is crucial for efficient breeding. Mather's (1949) scaling tests (A, B, and C) indicated that the simple additive-dominance model effectively explained the inheritance of the harvest index (HI), as all scales were non-significant ($P > 0.05$), suggesting selection in the F2 generation could enhance yield-associated traits (Kabbia et al., 2017). However, significant deviations ($P < 0.05$) for traits such as pod and seed count, biomass yield, and phenological traits under both well-watered (WW) and water-stressed (WS) conditions indicated the presence of maternal effects and gene interactions (Warnock et al., 1998; Kabbia et al., 2017).

Epistatic interactions, including additive × additive (i), additive × dominance (j), and dominance × dominance (l), were detected, suggesting the need for recurrent selection in later generations. Dominance effects were more pronounced than additive effects for traits like pod and seed count, biomass yield, and flowering time, indicating a significant role of dominance inheritance (Abd El-Haleem et al., 2010; Karademir & Gencer, 2010). Conversely, HI and emergence timing showed stronger additive effects, supporting early generation selection (Jagtap, 1986).

Negative additive × additive (i) or additive × dominance (j) values suggested gene dispersion in parents (Mather & Jinks, 1982; Kabbia et al., 2017). Traits exhibiting opposite dominance (d) and dominance × dominance (l) values, such as pod count and biomass yield, indicated duplicated epistasis, necessitating inter-mating to break undesirable linkages (Abdul-Hafeez et al., 2007; El-Beially & Mohamed, 2008). Narrow-sense heritability estimates were lower than broad-sense heritability, indicating non-additive gene action, with low heritability for pod yield and HI suggesting a focus on yield components rather than direct yield improvement (Girdthai et al., 2012). However, high heritability for biomass weight, seed yield, and SCMR 80 DAP suggested additive gene control, supporting heterosis breeding (Holbrook et al., 1989; Songsri et al., 2008).

Variation (Heritability) for Groundnut Traits Based on F2 and BC Populations

Analysis of F2 and backcross (BC) populations showed BC1.1 (Chinese/Ndogba/Chinese) performed best in WW conditions, demonstrating high plant height at harvest and maturity (Table 3). High broad-sense heritability values indicated the significance of additive and non-additive genetic factors in trait inheritance under different conditions (Rao et al., 2012; Gowda et al., 2013; Morales et al., 2020). The findings support breeding programs aimed at improving groundnut productivity and drought tolerance (Kabir et al., 2023).

Generation Mean Performance for Growth Parameters Under WW and WS Conditions

Well-Watered Conditions (WW)

Population 1 performance under WW conditions (Table 4) showed that Chinese parent (P1) had the fastest emergence (6 days), flowering in 21 days, and maturing in 87 days with a final plant height of 53.3 cm. Ndogba parent (P2) took 7 days to emerge, 22 days to flower, and matured in 89 days, with a harvest height of 32.0 cm. The F1 generation showed intermediate performance, flowering in 24 days, maturing in 90 days, and reaching 46.7 cm at harvest. F2 plants had a shorter height at harvest (36.3 cm) but similar flowering duration. BC1.1 (Chinese/Ndogba/Chinese) performed best, maturing in 94 days and reaching 58.7 cm at harvest. BC1.2 (Chinese/Ndogba/Ndogba) emerged fastest (6 days) but took longer to flower (27 days), reaching 49.0 cm at harvest.

Water-Stressed Conditions (WS)

Under WS conditions, P1 took 8 days to emerge, 25 days to flower, and matured in 92 days with a harvest height of 57.3 cm, while P2 matured in 89 days with a harvest height of 42.0 cm. The F1 generation displayed comparable flowering (26 days) and harvest height (46.7 cm) to WW conditions. F2 plants had a shorter harvest height (31.3 cm). BC1.1 again outperformed others, maturing in 93 days with a harvest height of 56.7 cm, while BC1.2 matured in 90 days and reached 47.0 cm at harvest.

BC1.1's superior performance across both conditions aligns with findings that selecting well-performing parents enhances progeny drought tolerance and yield stability (Upadhyaya et al., 2011; Kakeeto et al., 2020). Research by Anjum et al. (2011) also emphasizes drought tolerance as a complex trait influenced by physiological resilience, growth patterns, and genetic factors. The strong genetic combination of BC1.1 suggests an effective strategy for stress-resilient crop development (Morales et al., 2020).

Generation Mean Performance for Growth Parameters in Ghanaian Landraces

Under WW conditions, Ghanaian landraces Sinkara (P1) and Chaco-pag (P2) exhibited an erect/bunch growth habit. Chaco-pag outperformed Sinkara in emergence (7 vs. 8 days), flowering height (16.6 cm vs. 11.0 cm), and harvest height (50.7 cm vs. 47.7 cm). The F1 and F2 generations retained their growth habit, with F1 maturing in 90 days and flowering in 28 days. BC1.2 (Sinkara/Chaco-pag/Chaco-pag) displayed the highest flowering height (15.13 cm), indicating superior growth under optimal water conditions.

Under WS conditions, P2 (Chaco-pag) emerged earlier (7 days) and flowered sooner (25 days) than P1 (Sinkara), which emerged in 9 days and flowered in 29 days.

Despite slower emergence, Sinkara exhibited greater height at flowering (16.8 cm vs. 11.6 cm) and harvest (57.2 cm vs. 55.7 cm). BC1.2 maintained strong performance, with growth characteristics favorable for water-stressed environments.

CONCLUSION

The evaluation of different groundnut varieties, particularly 'Sinkara' and 'Chinese,' revealed high pod yield, seed yield, and biomass production under both well-watered (WW) and water-stressed (WS) conditions. However, drought stress significantly reduced pod yield, biomass, and seed weight, while specific chlorophyll measurements (SCMR 60 and SCMR 80 DAP) increased, suggesting a physiological response to water deficit.

Heritability estimates varied across traits, ranging from 7% to 96%. Notably, dry biomass weight (96%), seed yield (89%), and seed weight (69%) exhibited high heritability, indicating strong genetic control and the potential for effective selection in breeding programs. Furthermore, the significant positive correlation between pod yield and harvest index under both water regimes suggests that simultaneous improvement of these traits is feasible.

Generation mean and variance analyses demonstrated that pod yield, seed yield, and biomass weight were primarily influenced by additive and dominance gene effects. Additionally, the presence of non-allelic interactions additive × additive, additive × dominance, and dominance × dominance highlights the complexity of genetic control governing these traits. These findings underscore the importance of integrating both additive and non-additive genetic effects in breeding strategies aimed at improving drought tolerance and yield potential in groundnut.

REFERENCES

Abd El-Haleem, S. H. M., and Ghanem, S. M., 2010. Quantitative genetic analysis of yield and yield components in Egyptian cotton (Gossypium barbadense L.). African Journal of Agricultural Research, 5(5), 286-292.

Abdul-Hafeez, R. M., and Ibrahim, S. E., 2007. Genetic behavior of yield and its components in cotton (Gossypium hirsutum L.). World Journal of Agricultural Sciences, 3(5), 586-591.

Anjum, S. A., Xie, X. Y., Wang, L. C., Saleem, M. F., Man, C., and Lei, W., 2011. Morphological, physiological and biochemical responses of plants to drought stress. African journal of agricultural research, 6(9), 2026-2032.

Arunyanark, A., Jogloy, S., Akkasaeng, C., Vorasoot, N., Wongkaew, S., Patanothai, A., and Holbrook, C. C., 2008. Heritability of early leaf spot resistance and genotypic correlations with agronomic traits in peanut. Asian Journal of Plant Sciences, 7(5), 498-505.

Begna, T., 2021. Combining ability and heterosis in plant improvement. Open Journal of Plant Science, 6(1), 108-117.

Bhatnagar-Mathur, P., Rao, J. S., and Sharma, K. K., 2007. Genetic engineering for abiotic stress tolerance in groundnut (Arachis hypogaea L.): Current status and future prospects. Plant Biotechnology Journal, 5(5), 543-558.

Bindu Madhava, H., Sheshshayee, M. S., Shankar, A. G., Prasad, T. G., and Udayakumar, M., 2003. Use of SPAD chlorophyll meter to assess transpiration efficiency of peanut. Agronomy Journal, 95(1), 212-217.

Cavalli, L. L., 1952. An analysis of linkage in quantitative inheritance. In Quantitative inheritance (pp. 135-144). HMSO. correlation among some shoot traits and transpiration efficiency in a groundnut germplasm. Journal of Agricultural Science, 137(1), 81-86.

Dietz, K. J., Zörb, C., and Geilfus, C. M., 2021. Drought and crop yield. Plant Biology, 23(6), 881-893.

Dong, X. J., Yin, Y., Yang, Q., and Wang, M. L., 2006. Identification and genetic analysis of water-use efficiency and drought resistance in groundnut (Arachis hypogaea L.). Plant Breeding, 125(3), 268-271.

El-Beially, S. A., and Mohamed, I. M., 2008. Gene effects and combining ability in cotton (Gossypium hirsutum L.). Asian Journal of Plant Sciences, 7(7), 664-668.

Esmail, R. M. (2007). Genetic studies on yield and its components in cotton (Gossypium barbadense L.). Journal of Applied Sciences Research, 3(10), 1124-1129.

Fita, A., Rodríguez-Burruezo, A., Boscaiu, M., Prohens, J., and Vicente, O., 2015. Breeding and domesticating crops adapted to drought and salinity: a new paradigm for increasing food production. Frontiers in Plant Science, 6, 978.

Fonceka, D., Tossim, H. A., Rivallan, R., Vignes, H., Faye, I., Ndoye, O., ... and Courtois, B., 2012. Genetic mapping of wild introgressions into cultivated peanut: a way toward enlarging the genetic basis of a recent allopolyploid. BMC Plant Biology, 12(1), 26.

Gautami, B., Pandey, M. K., Vadez, V., Nigam, S. N., Ratnakumar, P., Krishnamurthy, L., ... and Varshney, R. K., 2012. Genetic architecture of drought and heat tolerance in groundnut (Arachis hypogaea L.). International Journal of Plant Genomics, 2012.

Girdthai, T., Jogloy, S., Kesmala, T., Vorasoot, N., Akkasaeng, C., Wongkaew, S., and Patanothai, A., 2010. Heritability of root traits and correlation with harvest index in peanut under terminal drought condition. Asian Journal of Plant Sciences, 9(4), 215-222.

Girdthai, T., Jogloy, S., Vorasoot, N., Akkasaeng, C., Wongkaew, S., Patanothai, A., and Holbrook, C. C., 2012. Inheritance of the physiological traits for drought resistance under terminal drought conditions and genotypic correlations with agronomic traits in peanut.

Gowda, M. V. C., Nigam, S. N., Chandra, S., and Reddy, A. G. S., 2013. Characterization of the drought tolerance traits of a new groundnut variety ICGV 91114. Journal of SAT Agricultural Research, 11, 1-5.

Grandawa, M. M., 2014, May. Characterisation of physico-chemical properties of Arachis hypogaea L. shells (groundnut) as environmental remidation. In International conference on chemical, biological, and environmental sciences (ICCBES'14) (pp. 12-13).

Hadebe, S. T., Modi, A. T., and Mabhaudhi, T., 2017. Drought tolerance and water use of cereal crops: A focus on sorghum as a food security crop in sub-Saharan Africa. Journal of Agronomy and Crop Science, 203(3), 177-191.

Hamidou, F., Halilou, O., and Vadez, V., 2012. Assessment of groundnut under combined heat and drought stress. Journal of Agronomy and Crop Science, 198(1), 1-12.

Hendawy, M. A., and Sadek, S. E., 2009. Genetic analysis of some quantitative traits in cotton (Gossypium barbadense L.). Research Journal of Agriculture and Biological Sciences, 5(6), 1111-1116.

Holbrook, C. C., and Stalker, H. T., 2003. Peanut breeding and genetics. In Peanuts: Genetics, Production, and Utilization, (pp. 111-131).

Holbrook, C. C., Isleib, T. G., Ozias-Akins, P., Chu, Y., and Knauft, D. A., 2009. Development and phenotyping of a recombinant inbred line population for breeding improved drought tolerance in peanut. Plant Genetic Resources, 7(2), 101-108.

Holbrook, C. C., Kvien, C. K., and Rucker, K. S., 2009. Heritability of drought tolerance in peanut. Peanut Science, 36(1), 16-20.

Holbrook, C. C., Wilson, D. M., and Anderson, W. F., 1989. Heritability of aflatoxin production in groundnut. Peanut Science, 16(1), 30-33.

Jagtap, V. S., 1986. Additive and dominance gene action for seed yield and its components in groundnut (Arachis hypogaea L.). Journal of Maharashtra Agricultural Universities, 11(3), 349-351.

Jaleel, C. A., Manivannan, P., Wahid, A., Farooq, M., Somasundaram, R., and Panneerselvam, R., 2009. Drought stress in plants: A review on morphological characteristics and pigments composition. International Journal of Agriculture and Biology, 11(1), 100-105.

Kabbia, I. B., Haougui, A., Hadi, A. I., and Adam, S., 2017. Influence of water stress and field capacities on yield and water use efficiency of groundnut varieties (Arachis hypogaea L.). Agronomy, 9(8), 460.

Kabir, M., Habiba, U. E., Khan, W., Shah, A., Rahim, S., Patricio, R., ... and Shafiq, M., 2023. Climate change due to increasing concentration of carbon dioxide and its impacts on environment in 21st century; a mini review. Journal of King Saud University-Science, 35(5), 102693.

Kakeeto, R., Melis, R., Biruma, M., and Sibiya, J., 2020. Gene action governing the inheritance of drought tolerance and selected agronomic traits in Ugandan groundnut (Arachis hypogaea L.) lines under drought environment. Euphytica, 216(1), 1.

Karademir, C., and Gencer, O., 2010. Inheritance of yield and related traits in cotton, Gossypium hirsutum L. Turkish Journal of Field Crops, 15(2), 110-116.

Mather, K., 1949. Biometrical Genetics: The Study of Continuous Variation. Dover Publications.

Mather, K., and Jinks, J. L., 1982. Introduction to Biometrical Genetics. Chapman and Hall, London.

Mert, M., and Soysal, Y., 2003. Genetic analysis of yield and fiber traits in upland cotton (Gossypium hirsutum L.) by using generation mean analysis. Pakistan Journal of Botany, 35(2), 129-136.

Morales, F., Ancín, M., Fakhet, D., González-Torralba, J., Gámez, A. L., Seminario, A., ... and Aranjuelo, I., 2020. Photosynthetic metabolism under stressful growth conditions as a bases for crop breeding and yield improvement. Plants, 9(1), 88.

Morales, M. S., Morán, M. A., Vera, M. A., and Balzarini, M. G., 2020. Drought tolerance in cereal crops: Genetic strategies to improve yield and quality. Journal of Cereal Science, 93, 102943.

Mulder, H. A., Gienapp, P., and Visser, M. E., 2016. Genetic variation in variability: Phenotypic variability of fledging weight and its evolution in a songbird population. Evolution, 70(9), 2004-2016.

Murtaza, N., 2005. Genetic analysis of yield and its components in upland cotton (Gossypium hirsutum L.). Pakistan Journal of Biological Sciences, 8(4), 592-595.

Mwamahonje, A., Eleblu, J. S. Y., Ofori, K., Deshpande, S., Feyissa, T., and Tongoona, P., 2021. Drought tolerance and application of marker-assisted selection in sorghum. Biology, 10(12), 1249.

Nageswara Rao, R. C., Talwar, H. S., and Wright, G. C., 2001. Rapid assessment of specific leaf area and chlorophyll content in peanut cultivars. Agronomy Journal, 93(3), 582-586.

Nautiyal, P. C., Ravindra, V., Rathnakumar, A. L., and Joshi, Y. C., 2002. Genetic and physiological traits in groundnut (Arachis hypogaea L.) associated with drought tolerance. Field Crops Research, 75(2), 129-139.

Nigam, S. N., and Aruna, R., 2008. Genetic enhancement for abiotic stress tolerance in groundnut (Arachis hypogaea L.). Journal of SAT Agricultural Research, 6, 1-13.

Nigam, S. N., Dwivedi, S. L., and Gibbons, R. W., 2001. Groundnut breeding: Constraints, achievements and future prospects. Plant Breeding Abstracts, 71(5), 362-370.

Oppong-Sekyere, D., Akromah, R., Appiah-Kubi, Z., and Tetteh, A. Y., 2019. Genetic analysis of agronomic traits in some groundnut (Arachis hypogaea L.) genotypes. African Journal of Agricultural Research, 14(5), 230-240.

Pandey, M. K., Roorkiwal, M., Singh, V. K., Ramalingam, A., Kudapa, H., Thudi, M., ... and Varshney, R. K., 2014. Emerging genomic tools for legume breeding: Current status and future prospects. Frontiers in Plant Science, 5, 390.

Puangbut, D., Jogloy, S., Kesmala, T., Vorasoot, N., Akkasaeng, C., Patanothai, A., and Puppala, N., 2011. Heritability of early season drought resistance traits and genotypic correlation of early season drought resistance and agronomic traits in peanut. SABRAO Journal of Breeding and Genetics, 43(2).

Rao, R. N., Sheshshayee, M. S., Karaba, N. N., Sreevathsa, R., Rama, N., Kumaraswamy, S., ... and Udayakumar, M., 2012. Groundnut: Genetic Approaches to Enhance Adaptation of Groundnut (Arachis Hypogaea, L.) to Drought. Improving Crop Productivity in Sustainable Agriculture, 303-359.

Raza, A., Mubarik, M. S., Sharif, R., Habib, M., Jabeen, W., Zhang, C., ... and Varshney, R. K., 2023. Developing drought-smart, ready-to-grow future crops. The Plant Genome, 16(1), e20279.

Richardson, A. D., Duigan, S. P., and Berlyn, G. P., 2002. An evaluation of noninvasive methods to estimate foliar chlorophyll content. New Phytologist, 153(1), 185-194.

Sheshshayee, M. S., Bindumadhava, H., Ramesh, R., Prasad, T. G., Lakshminarayana, M. R., and Singh, R. K., and Narayanan, S. S., 1993. Biometrical Techniques in Plant Breeding. Kalyani Publishers.

Songsri, P., Jogloy, S., Vorasoot, N., Akkasaeng, C., Patanothai, A., and Holbrook, C. C., 2008. Root distribution of drought-resistant peanut genotypes in response to drought. Journal of Agronomy and Crop Science, 194(2), 92-103.

Spinoni, J., Barbosa, P., De Jager, A., McCormick, N., Naumann, G., Vogt, J. V., ... and Mazzeschi, M., 2019. A new global database of meteorological drought events from 1951 to 2016. Journal of Hydrology: Regional Studies, 22, 100593.

Tsaur, S. C., and Chen, Y. T., 1989. Inheritance of yield and its components in peanut (Arachis hypogaea L.). Botanical Bulletin of Academia Sinica, 30(1), 31-37.

Udayakumar, M., 2006. Leaf chlorophyll content derived SPAD value as an indicator of drought tolerance in groundnut. Journal of SAT Agricultural Research, 2(1), 1-7.

Upadhyaya, H. D., Bramel, P. J., Ortiz, R., and Singh, S., 2001. Developing a core collection of peanut (Arachis hypogaea L.) using taxonomical, geographical, and morphological descriptors. Genetic Resources and Crop Evolution, 48(6), 625-632.

Upadhyaya, H. D., Dwivedi, S. L., Vadez, V., Hamidou, F., Singh, S., Varshney, R. K., and Liao, B., 2011. Multiple resistant and nutritionally dense germplasm identified from mini core collection in peanut. Crop Science, 51(4), 1337-1354.

Upadhyaya, H. D., Sharma, S., Singh, S., and Singh, M., 2011. Inheritance of drought resistance related traits in two crosses of groundnut (Arachis hypogaea L.). Euphytica, 177, 55-66.

Vieira, S. D., Araujo, A. L., Souza, D. C., Resende, L. V., Leite, M. E., and Resende, J. T., 2019. Heritability and combining ability studies in strawberry population. Journal of Agricultural Science, 11(4), 57-469.

Warnock, D. F., and Kidane-Mariam, H. M., 1998. Breeding for drought tolerance in peanut. Advances in Agronomy, 64, 1-41.

Xue, J., Zhou, S., Wang, W., Huo, L., Zhang, L., Fang, X., and Yang, Z., 2018. Water availability effects on plant growth, seed yield, seed quality in Cassia obtusifolia L., a medicinal plant. Agricultural Water Management, 195, 104-113.