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Combining Ability, Heritability and Heterosis for Grain and Biomass Yield in Cowpea (*Vigna unguiculata* L. Walp) Hybrids Evaluated under Drought Stress

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Abstract

Developing dual-purpose cowpea varieties that combine high grain and biomass yields is important for food and nutritional security in drought-prone environments. This study evaluated combining ability, heterosis, and heritability among six cowpea parental lines and 10 F_1 hybrids produced using a half-diallel mating design under drought-stress conditions. General combining ability (GCA), specific combining ability (SCA), broad-sense heritability, narrow-sense heritability, and heterosis were estimated to assess the relative contributions of additive and non-additive genetic effects. Significant GCA and SCA effects were observed for all measured traits. The GCA:SCA ratio ranged from 0.41 for grain yield to 4.63 for pod width, indicating a greater contribution of non-additive effects to grain yield and a stronger additive influence on pod width. Broad-sense heritability ranged from 0.90 to 0.99, whereas narrow-sense heritability ranged from 0.28 to 0.79, showing that the potential response to selection differed among traits. Heterosis for grain and biomass yields varied widely among hybrids and between trials. MA67 × NA60 showed consistently positive

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heterosis for both grain and biomass yields, while MA50 × MA67 also showed positive heterosis for both traits across the two trials. The findings indicate that parent selection and hybrid evaluation should be combined when breeding drought-tolerant, dual-purpose cowpea, with further testing required across seasons and locations.

Keywords: Vigna unguiculata; combining ability; general combining ability; specific combining ability; heterosis; heritability; grain yield; biomass yield; drought stress.

1. Introduction

Cowpea (*Vigna unguiculata* L. Walp.) is a key legume crop in tropical and subtropical regions, particularly in sub-Saharan Africa, where it provides an affordable source of protein, vitamins, and minerals for millions of people (Nounagnon et al., 2024). Beyond grain production, cowpea leaves, green pods, and immature seeds are widely consumed as vegetables, contributing to dietary diversity and nutritional security (da Silva et al., 2018). However, the increasing frequency of drought associated with climate change poses a major constraint to cowpea productivity, especially in semi-arid regions where water availability is limited (Ngalamu et al., 2023). The development of dual-purpose cowpea varieties capable of producing high grain and biomass yields offers a promising strategy for enhancing food and nutritional security under such conditions (Akplo et al., 2023). However, drought tolerance is a complex quantitative trait governed by multiple genes and strongly influenced by environmental interactions, making its improvement challenging (Nkomo et al., 2021; Bapela et al., 2022). Effective breeding for drought-resilient and dual-purpose traits requires a clear understanding of the underlying genetic architecture. A recent synthesis of drought-tolerance breeding in legumes emphasises the value of combining genotypic variability, heritable adaptive traits, and complementary conventional and molecular approaches when developing climate-resilient cultivars (Tejaswini et al., 2025).

Quantitative genetic tools such as heritability estimation, heterosis evaluation, and combining ability analysis are essential for guiding selection and hybridisation strategies. Heritability provides insight into the proportion of phenotypic variation attributable to genetic factors, whereas heterosis reveals the potential for hybrid vigour in specific crosses (Yadesa et al., 2022; Begna, 2021). Combining ability analysis, through GCA and SCA, further partitions genetic effects into additive and non-additive components, enabling the identification of superior parents and cross combinations (Gea & Currie, 2008). Heritability analysis also provides crucial information about the genetic basis of trait variation and the potential for genetic improvement through selection (Yadesa et al., 2022). High heritability estimates indicate that a significant proportion of the observed phenotypic variation is attributable to genetic factors, suggesting that selection for drought tolerance and dual-purpose characteristics may be effective. Understanding heritability patterns across traits helps breeders prioritise selection criteria and allocate resources efficiently within breeding programmes.

Although cowpea is predominantly a self-pollinating crop, heterosis, or hybrid vigour, remains an important genetic phenomenon that can be exploited in breeding programmes to enhance performance (Begna, 2021). The magnitude of heterosis for traits such as drought tolerance and dual-purpose utility (grain and vegetable use) provides insight into the genetic potential of specific cross combinations. Although the commercial exploitation of hybrid vigour is limited in self-pollinating crops such as cowpea because of challenges in hybrid seed production, significant heterotic effects can still inform parental selection and guide population-improvement strategies. Systematic evaluation of heterosis under diverse environmental and stress conditions helps to elucidate the genetic mechanisms underlying superior hybrid performance, thereby aiding the development of improved breeding lines (Xiao et al., 2021).

Combining ability analysis, encompassing both GCA and SCA, provides detailed information about the breeding value of individual genotypes and the performance of specific cross combinations (Gea & Currie, 2008). GCA effects reflect the average performance of a genotype across multiple crosses, indicating its overall breeding value and suitability as a parent in breeding programmes (Gea & Currie, 2008). SCA effects represent the deviation of specific cross combinations from the performance expected on the basis of parental GCA values, highlighting combinations with exceptional performance resulting from favourable gene interactions. Recent diallel studies in cowpea have shown that additive and non-additive gene effects can differ among yield-related traits and stress environments, reinforcing the need to evaluate GCA, SCA, heritability, and heterosis

jointly when selecting parents and cross combinations (Ezin et al., 2023; Jou-Nteufa & Ceyhan, 2024; Matjeke et al., 2025).

An unresolved need is the integrated evaluation of how additive and non-additive genetic effects relate simultaneously to grain and biomass yields in cowpea hybrids under drought stress. Addressing this gap is necessary to distinguish parents and cross combinations with potential for dual-purpose improvement under water-limited conditions. Despite the importance of these genetic parameters, information on combining ability, heritability, and heterosis remains limited, particularly for dual-purpose traits such as grain and biomass yields (Ezin et al., 2023; Matjeke et al., 2025). This limitation reduces the efficiency of breeding programmes targeting drought-prone environments. Therefore, this study aimed to assess combining ability, heterosis, and heritability among selected cowpea lines using a half-diallel mating design under drought-stressed conditions to identify superior parents and hybrids for dual-purpose productivity.

2. Materials and Methods

2.1 Study Site

The $F_{1\ hybrids}$ and their parents were evaluated at Chuka University's Kairini Farm. The farm is located at latitude 00°23′51.4″ S and longitude 037°46′24.0″ E, at approximately 1,400 m above sea level. The region receives approximately 300–700 mm of rainfall annually and has an average temperature of 28 °C. The area has deep, well-weathered volcanic foot-ridge soils with moderate to high inherent fertility (Jaetzold et al., 2006).

2.2 Plant Materials

Six cowpea accessions were selected for the production of F_1 genotypes. Selection was based on the extreme performance of 50 cowpea accessions with respect to earliness, drought tolerance, pest attack, and leaf-production potential. The set of 50 cowpea accessions included 21 accessions from the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria; 27 from the National Gene Bank of Kenya, KALRO-Muguga; and two farmer-preferred varieties.

2.3 Crossing Design

A half-diallel mating design was used to develop 10 F_1 hybrids from six parental genotypes. Initially, 15 hybrids were expected from the six parents; however, because of flower abortion and cross-incompatibility among some parental combinations, only 10 F_1 hybrids were successfully produced (Section 2.3.1) and used for subsequent field evaluation and genetic analysis.

2.3.1 Development of F_1 Hybrids

Six selected cowpea accessions (MA50, NA11, MA67, KK06, NA60, and NA20) were planted in the field to develop F_1 hybrids. The accessions were planted at a spacing of 60 cm × 30 cm. Forceps with sharp, precisely pointed tips were used to emasculate female flowers. To prevent contamination and the transfer of undesired pollen, the forceps were sanitised with 70% alcohol after each use. In cowpea, a flower bud ready for pollination is slightly paler than its usual deep-green colour (Ogunkanmi et al., 2007). Mature flowers were identified during the morning or afternoon. Each flower was then emasculated, and pollen from a selected male parent was manually transferred to the emasculated female parent. After pollination, a small tag indicating the codes of the male and female parents was attached to the peduncle beneath the pollinated bud. Owing to flower abortion and cross-incompatibility among some parental combinations, only 10 of the 15 possible F_1 hybrids were developed.

2.4 Experimental Design

A randomised complete block design (RCBD) with three replicates was used to evaluate the F_1 cowpea genotypes and their parents in the field.

2.4.1 Drought Treatment

The 10 developed F_1 cowpea hybrids were sown on ridges at a spacing of 60 cm × 30 cm. The experimental field was maintained free of weeds, pests, and diseases. The plants received adequate irrigation (800–1,200 mL

per plant) for up to 28 days after sowing to ensure uniform establishment. Thereafter, terminal drought stress was imposed by reducing irrigation to 175–350 mL per plant every five days. This irrigation regime simulated seasonal rainfall of approximately 100–200 mm over a 90-day growing period. The treatment was intended to simulate the moisture-limited conditions characteristic of arid and semi-arid environments. The genotypes were evaluated to assess their responses to drought stress and identify drought-tolerant lines. Drought tolerance was screened according to Watanabe et al. (1997).

2.5 Data Collection

2.5.1 Morphological Characterisation

Data were collected from three randomly selected plants in each row using the International Board for Plant Genetic Resources (IBPGR) cowpea descriptor. Quantitative data included biomass and grain yields (IBPGR, 1983). To evaluate dual-purpose genotypes, biomass (leaf-production) data were collected immediately before pod setting by uprooting whole plants in two replicates. The plants were defoliated, and the leaves, stems, and roots were weighed separately. Grain yield was determined at the end of the experiment using the remaining plants. All pods from each accession were harvested and weighed.

2.6 Data Analysis

2.6.1 Evaluation of Combining Ability, Heritability and Heterosis of Developed F_1 Hybrids

2.6.1.1 Computation of Genetic Parameters

Combining ability analysis was performed using Griffing's Method II, Model I (Griffing, 1956), which partitions genetic variation into GCA and SCA effects, thereby facilitating the identification of the additive and non-additive gene actions controlling the traits of interest.

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + e_{ij}$$

where: Y_{ij} = the mean performance of the i^{th} parental line mated to the j^{th} parental line;
μ = the population mean effect common to all observations;
g_i and g_j = the general combining ability effects of the i^{th} and j^{th} parents, respectively;
s_{ij} = the SCA effect for the cross between i and j; and
e_{ij} = the random error.

2.6.1.2 Estimation of Component Variances and Their Genetic Interpretations

Using the expectations of mean squares (EMS) from the ANOVA under Griffing's effects model (Model II), the GCA and SCA variance components were estimated as follows:

$$\sigma^2_{GCA} = \frac{MS_{GCA} - MS_{SCA}}{2p}$$

$$\sigma^2_{SCA} = \frac{MS_{SCA} - MS_{Error}}{r}$$

where:
MS_{GCA} = the mean square for general combining ability;
MS_{SCA} = the mean square for specific combining ability;
MS_{Error} = the residual mean square;
p = the number of parents; and
r = the number of replications.

These variance components were subsequently used to assess the relative contributions of additive and non-additive genetic effects governing the traits under study. A higher GCA variance than SCA variance indicates

the predominance of additive gene action, which is favourable for selection-based breeding strategies. In contrast, a greater SCA variance suggests that non-additive genetic effects, such as dominance or epistasis, play a more significant role in trait expression. The GCA:SCA ratio was used as an indicator of the relative importance of additive versus non-additive gene action for each trait, providing critical insight into the underlying genetic architecture and guiding the choice of appropriate breeding approaches.

2.6.1.3 Estimation of Heritability

Broad-sense heritability (H) was estimated as follows:

$$H = \frac{\sigma_g^2}{\sigma_p^2}$$

where: σ_g^2 is the genetic variance.
σ_p^2 is the phenotypic variance.

Narrow-sense heritability (h^2) was estimated as follows:

$$h^2 = \frac{\sigma_A^2}{\sigma_p^2}$$

where: σ_A^2 is the additive genetic variance.
σ_p^2 is the phenotypic variance.

2.6.1.4 Estimation of Heterosis

Heterosis was estimated according to Hallauer and Miranda Filho (1988) as follows:

$$H = \frac{\overline{F_1} - \overline{M_p}}{\overline{M_p}} x100$$

where: H is heterosis;
$\overline{F_1}$ is the mean performance of the F_1 hybrid.
$\overline{M_p}$ is the mean performance of mid-parent.

2.6.1.5 Estimation of Phenotypic Correlations

The phenotypic correlation (r_p) between characters X and Y was calculated as follows:

$$rp = Cov(p_x, p_y)$$

$$\sqrt{\sigma^2 P_x, \sigma^2 P_y}$$

3. Results and Discussion

3.1 Determination of Combining Ability, Heritability and Heterosis of Developed F_1 Cowpea Genotypes

3.1.1 Combining Ability and Heritability

The analysis based on Griffing's Method II showed that the fitted model adequately explained the observed variation in all measured traits ($p < 0.05$). Both GCA and SCA had significant effects ($p < 0.05$) on all measured variables, indicating contributions from additive and non-additive genetic components to trait expression.

The GCA estimates ranged from 3.64 for the drought-tolerance index to 28956.18 for grain yield, whereas the SCA estimates ranged from 6.59 for the drought-tolerance index to 70121.18 for grain yield (Table 1). The GCA:SCA ratio ranged from 0.41 for grain yield to 4.63 for pod width, suggesting a predominance of non-additive effects for grain yield and a greater influence of additive effects on pod width.

Table 1. General combining ability, specific combining ability and heritability of various traits of cowpea genotypes under drought stress

Variable	GCA	SCA	GCA:SCA ratio	H	h^2
Grain yield	28956.18	70121.18	0.41	0.95	0.28
100 Seed weight	7.66	4.36	1.76	0.90	0.58
Pod width	44657.65	9674.58	4.63	0.95	0.79
Days to 50% flowering	8.19	16.62	0.49	0.96	0.32
Pod length	5.44	9.04	0.60	0.99	0.37
Number of pods per plant	2743.50	3284.42	0.84	0.99	0.46
Drought tolerance index	3.64	6.59	0.55	0.96	0.34
Number of seeds per pod	23.63	33.97	0.70	0.99	0.41

Where H = broad sense heritability and h^2 = narrow sense heritability

The GCA:SCA ratios for 100-seed weight and pod width exceeded one, confirming the greater importance of additive genetic variance. These results have important implications for breeding strategies, particularly for selecting suitable parents and designing appropriate improvement methods for each trait. The findings showed that, for grain yield, days to 50% flowering, pod length, number of pods per plant, drought-tolerance index, and number of seeds per pod, the SCA estimates were higher than the GCA estimates. This indicates that non-additive gene effects, such as dominance and epistasis, play a more significant role in the expression of these traits. The GCA:SCA ratios for these traits were less than one, further supporting the predominance of non-additive genetic variance. In contrast, for 100-seed weight and pod width, the GCA effects were greater than the SCA effects, suggesting that additive gene effects have a greater influence on these traits. The GCA:SCA ratios for both traits were greater than one, confirming the predominance of additive genetic variance.

Broad-sense heritability (H) estimates were generally high, ranging from 0.90 for 100-seed weight to 0.99 for pod width and several other traits, indicating substantial genetic control of phenotypic variation (Table 1). In contrast, narrow-sense heritability (h^2), which reflects the proportion of additive genetic variance, was comparatively lower, ranging from 0.28 for grain yield to 0.79 for pod width. These findings suggest that, although most traits are under strong genetic influence, the potential for genetic gain through selection varies; pod width showed high additive variance, whereas grain yield was more strongly influenced by non-additive effects. These findings are consistent with those of Pessoa et al. (2024), who reported that both additive and non-additive genetic effects influence the behaviour of inherited traits in cowpea. The results indicated that GCA and SCA varied for all measured characters, signifying the importance of both additive and non-additive genetic components in the present study. These results are also consistent with those of Owusu et al. (2018), who demonstrated variation in GCA and SCA for the 12 cowpea traits they evaluated.

These results highlight the complex genetic nature of the evaluated traits in cowpea. Combining ability indicates the breeding value of parental lines for generating hybrids and thus aids in identifying parents with high GCA and parental combinations with high SCA (Sprague & Tatum, 1942; Griffing, 1956). Traits such as 100-seed weight and pod width, which are predominantly controlled by additive genes, are more amenable to improvement through simple selection methods. However, traits such as grain yield and drought tolerance, which are influenced by non-additive effects, may require more sophisticated breeding strategies, such as hybridisation or marker-assisted selection, to achieve significant genetic gains. SCA effects, which are considered manifestations of non-additive gene action, are important for discriminating among crosses according to their genetic value as breeding materials, particularly for hybrid production. The high SCA values of these hybrids indicate that the expression of these traits is determined by dominance, epistasis, and other gene interactions (Griffing, 1956; Baker, 1978). In general, crosses showing highly significant and desirable SCA effects were associated with high performance for the respective traits in specific hybrids. This finding is consistent with that of Abd El-Azeem et al. (2021), who demonstrated the importance of SCA effects in developing superior hybrid varieties.

Broad-sense heritability was high for most traits, indicating that much of the observed phenotypic variation was attributable to genetic factors. However, most traits showed low to moderate narrow-sense heritability, suggesting that a large proportion of the genetic variance was attributable to dominance effects. The response to selection is greater for traits with higher narrow-sense heritability (Schmidt et al., 2019). Narrow-sense heritability reflects the proportion of phenotypic variance attributable to additive genetic variance alone (Falconer & Mackay, 1996). It is therefore a more direct measure of the potential response to selection. Traits with high broad-sense heritability but low narrow-sense heritability, such as grain yield, days to flowering, and pod length, suggest that, although these traits are genetically controlled, their improvement through selection may be limited by non-additive genetic effects or environmental variability. Traits with both high broad-sense and narrow-sense heritability, such as pod width and number of seeds per pod, are suitable candidates for selection because they have a substantial additive genetic component. High narrow-sense heritability has been associated with more accurate estimates of genetic gain, thereby substantially reducing the number of selection cycles in a breeding programme (Seck et al., 2023).

3.1.2 Heterosis

The results revealed substantial variation in heterosis for grain and biomass yields across genotypes and trials (Tables 2 and S1). In Trial 1, heterosis for grain yield ranged from -68.86 (KK06 X MA67) to 180.75 (MA50 X MA67), whereas heterosis for biomass yield ranged from -89.87 (MA50 X NA20) to 507.61 (MA67 X NA60) (Table 2). In Trial 2, heterosis for grain yield ranged from -60.15 (MA50 X NA20) to 227.48 (MA67 X NA60), whereas heterosis for biomass yield ranged from -72.51 (KK06 X NA11) to 316.19 (MA67 X NA60).

The hybrid MA50 X NA11 showed positive heterosis for biomass yield in both trials. The hybrids MA67 X NA60, KK06 X MA67, and MA50 X MA67 showed high heterosis for biomass or grain yield in one or both trials. The hybrid MA50 X MA67 showed positive heterosis for both grain and biomass yields in both trials. The hybrid MA67 X NA60 was notable for its consistently positive heterosis for grain and biomass yields across both trials, indicating relatively stable performance under drought stress. The hybrids MA50 X NA11 and KK06 X NA11 showed variable performance, with positive heterosis under some conditions and negative heterosis under others. Based on the heterosis estimates, MA67 X NA60, MA50 X MA67, MA50 X NA60, and NA20 X NA60 showed comparatively favourable grain-yield performance in at least one trial, whereas KK06 X MA67, MA67 X NA60, and MA50 X NA11 showed positive biomass heterosis in at least one trial.

Table 2. Heterosis of grain and biomass yield for 10 F_1 cowpea hybrid genotypes under drought-stress conditions in two trials

Genotypes	Yield Trial 1	Yield Trial 2	Biomass Trial 1	Biomass Trial 2
MA50 X NA11	38.29	-4.36	103.36	11.68
MA67 X NA60	4.07	227.48	507.61	316.19
KK06 X NA11	-20.41	745.14	8.22	-72.51
MA50 X MA67	180.75	142.37	463.24	25.35
MA50 X NA20	-5.81	-60.16	-89.87	-24.71
NA11 X NA60	-34.49	-21.88	-11.19	-53.87
MA50 X NA60	-13.72	94.68	1.52	113.54
NA20 X NA60	139.72	186.56	157.69	-26.84
MA67 X NA11	-39.38	135.98	27.21	-38.58
KK06 X MA67	-68.86	362.80	320.39	160.12

Where KK = Kakamega accessions, NA = IITA accessions, MA = NGBK-KALRO-Muguga accessions

The evaluated F_1 hybrid genotypes showed a wide range of heterosis estimates for grain and biomass yields. This variability reflects genetic diversity and differences in genotypic responses under drought stress. F_1 hybrid genotypes exhibiting high positive heterosis are indicative of strong SCA and thus of favourable non-additive gene interactions (Falconer & Mackay, 1996; Schmidt et al., 2019). Heterosis showed a stronger positive correlation with SCA than with GCA, indicating that SCA may serve as a useful predictor of heterotic potential in hybrid development (Yu et al., 2020). The high heterosis observed in certain hybrids, particularly under adverse conditions, suggests their potential use in breeding programmes aimed at improving drought tolerance and yield stability in cowpea. The genotype MA67 X NA60 appears particularly promising because of its consistently positive heterosis across both trials. Differential expression of heterosis in morphological traits is

largely attributable to complex interactions among a subset of loci controlling these traits (Farinati et al., 2023). The importance of genetic diversity in selecting parents for breeding programmes has also been repeatedly emphasised (Singh, 2005).

The range of heterosis estimates provides insight into the genetic potential of these hybrids and their adaptation to drought-stressed environmental conditions, which is important for selecting superior genotypes in breeding programmes. Burgess et al. (2023) demonstrated that selecting superior parents can improve crop growth and yield attributes. However, some crosses showed highly negative heterosis for grain and biomass yields. The observed negative heterosis could be attributed to genetic incompatibility or unfavourable gene interactions between the parental lines, which may reduce hybrid performance. When parental genotypes are excessively divergent or incompatible, the resulting hybrids may show poor vigour, reduced growth, or impaired physiological functions, leading to lower yields (Fujimoto et al., 2018; Calvo-Baltanás et al., 2021). Negative epistasis, in which interactions between genes from the parental lines adversely affect the hybrid, may reduce grain and biomass yields.

4. Conclusion

The study showed that additive and non-additive gene effects contributed to the inheritance of the evaluated agronomic traits in cowpea under drought stress. Pod width and 100-seed weight had GCA:SCA ratios greater than one, indicating a comparatively stronger additive genetic contribution and potential for improvement through selection. Grain yield, days to 50% flowering, pod length, number of pods per plant, drought-tolerance index, and number of seeds per pod had ratios below one, indicating a greater contribution of non-additive effects. Although broad-sense heritability was high for all traits, narrow-sense heritability varied substantially, with grain yield recording the lowest estimate. Heterosis also varied between hybrids and trials. MA67 × NA60 showed consistently positive heterosis for grain and biomass yields, while other crosses differed in the direction and magnitude of their responses. These results support the combined use of parental selection, evaluation of specific cross combinations, and further testing of promising hybrids under drought-prone conditions before their use in breeding programmes.

5. Limitations

The manuscript does not present parent-specific GCA effects, cross-specific SCA effects, full ANOVA tables, standard errors, or exact p-values. Drought stress was imposed through reduced watering, but soil-moisture measurements and stress-validation data were not reported. Future studies should report these parameters, clarify the number of hybrids, validate drought intensity, and evaluate promising crosses across seasons and locations.

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Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abd El-Azeem, M. E. M., Aly, R. S. H., El Sayed, W. M., & Hassan, N. A. (2021). Combining ability and gene action using 10 × 10 diallel crosses of ten maize inbred lines (*Zea mays* L.). *Journal of Plant Production, 12*(11), 1205–1211. https://doi.org/10.21608/jpp.2021.105615.1073

Akplo, T. M., Faye, A., Obour, A., Stewart, Z. P., Min, D., & Prasad, P. V. V. (2023). Dual-purpose crops for grain and fodder to improve nutrition security in semi-arid sub-Saharan Africa: A review. *Food and Energy Security, 12*(5), e492. https://doi.org/10.1002/fes3.492

Baker, R. J. (1978). Issues in diallel analysis. *Crop Science, 18*(4), 533–536. https://doi.org/10.2135/cropsci1978.0011183X001800040001x

Bapela, T., Shimelis, H., Tsilo, T. J., & Mathew, I. (2022). Genetic improvement of wheat for drought tolerance: Progress, challenges and opportunities. *Plants, 11*(10), 1331. https://doi.org/10.3390/plants11101331

Begna, T. (2021). Combining ability and heterosis in plant improvement. *Open Journal of Plant Science, 6*(1), 108–117. https://doi.org/10.17352/ojps.000043

Burgess, A. J., Masclaux-Daubresse, C., Strittmatter, G., Weber, A. P. M., Taylor, S. H., Harbinson, J., Yin, X., Long, S., Paul, M. J., Westhoff, P., Loreto, F., Ceriotti, A., Saltenis, V. L. R., Pribil, M., Nacry, P., Scharff, L. B., Jensen, P. E., Muller, B., Cohan, J. P., & Baekelandt, A. (2023). Improving crop yield potential: Underlying biological processes and future prospects. *Food and Energy Security, 12*(1), e435. https://doi.org/10.1002/fes3.435

Calvo-Baltanás, V., Wang, J., & Chae, E. (2021). Hybrid incompatibility of the plant immune system: An opposite force to heterosis equilibrating hybrid performances. *Frontiers in Plant Science, 11*, 576796. https://doi.org/10.3389/fpls.2020.576796

da Silva, A. C., da Costa Santos, D., Teixeira Junior, D. L., da Silva, P. B., dos Santos, R. C., & Siviero, A. (2018). Cowpea: A strategic legume species for food security and health. In J. C. Jimenez-Lopez and A. Clemente (Eds.), *Legume seed nutraceutical research*. IntechOpen. https://doi.org/10.5772/intechopen.79006

Ezin, V., Tossou, T. A. W., Chabi, I. B., & Ahanchede, A. (2023). Diallel analysis of cowpea (*Vigna unguiculata* (L.) Walp.) genotypes under water deficit stress. *BMC Plant Biology, 23*, Article 539. https://doi.org/10.1186/s12870-023-04508-0

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th ed.). Longman. https://search-library.ucsd.edu/discovery/fulldisplay/alma991015366599706535/01UCS_SDI%3AUCSD

Farinati, S., Scariolo, F., Palumbo, F., Vannozzi, A., Barcaccia, G., & Lucchin, M. (2023). Heterosis in horticultural crop breeding: Combining old theoretical bases with modern genomic views. *Frontiers in Horticulture, 2*, 1250875. https://doi.org/10.3389/fhort.2023.1250875

Fujimoto, R., Uezono, K., Ishikura, S., Osabe, K., Peacock, W. J., & Dennis, E. S. (2018). Recent research on the mechanism of heterosis is important for crop and vegetable breeding systems. *Breeding Science, 68*(2), 145–158. https://doi.org/10.1270/jsbbs.17155

Gea, L., & Currie, A. (2008, September 9–12). General combining ability (GCA) and specific combining ability (SCA) in *Actinidia chinensis*: Implications for breeding population management and varietal selection [Conference presentation]. *18th EUCARPIA General Congress: Modern Variety Breeding for Present and Future Needs*, Valencia, Spain.

Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences, 9*(4), 463–493. https://doi.org/10.1071/BI9560463

Hallauer, A. R., & Miranda Filho, J. B. (1988). *Quantitative genetics in maize breeding* (2nd ed.). Iowa State University Press.

International Board for Plant Genetic Resources. (1983). *Descriptors for cowpea*. https://cgspace.cgiar.org/items/da6bbbb9-19d9-4cb5-8f03-8eb9f2c3d1c8

Jaetzold, R., Schmidt, H., Hornetz, B., & Shisanya, C. (2006). *Farm management handbook of Kenya: Vol. II. Natural conditions and farm management information: Part C, East Kenya, Subpart C2, Coast Province* (2nd ed.). Ministry of Agriculture, Kenya. https://edepot.wur.nl/487561

Jou-Nteufa, C., & Ceyhan, E. (2024). Genetic analysis of seed yield and some traits in cowpea using diallel analysis. *Turkish Journal of Agriculture and Forestry, 48*(2), 278–293. https://doi.org/10.55730/1300-011X.3180

Matjeke, B. M., Labuschagne, M., Gerrano, A. S., Minnaar-Ontong, A., & Mbuma, N. W. (2025). Cowpea genetic analysis: Integrating heritability, combining ability, and heterosis for grain yield and morphological traits. *Euphytica, 221*, Article 96. https://doi.org/10.1007/s10681-025-03520-9

Ngalamu, T., Galla, J. O., Ofori, K., & Meseka, S. K. (2023). Genetic improvement for development of climate-resilient food legume crops: Relevance of the cowpea breeding approach in the improvement of food legume crops for the future. In M. Z. Hossain, H. M. Anawar, & D. R. Chaudhary (Eds.), *Climate change and legumes: Stress mitigation for sustainability and food security* (pp. 97–120). CRC Press. https://doi.org/10.1201/9781003214885-7

Nkomo, G. V., Sedibe, M. M., & Mofokeng, M. A. (2021). Production constraints and improvement strategies of cowpea (*Vigna unguiculata* L. Walp.) genotypes for drought tolerance. *International Journal of Agronomy, 2021*, Article 5536417. https://doi.org/10.1155/2021/5536417

Nounagnon, M., Roko, G., Agbodjato, N. A., Dah-Nouvlessounon, D., Babalola, O. O., & Baba-Moussa, L. (2024). Cowpea (*Vigna unguiculata*). In R. Chandora, T. Basavaraja, & A. Pratap (Eds.), *Potential pulses: Genetic and genomic resources* (pp. 58–77). CABI. https://doi.org/10.1079/9781800624658.0004

Ogunkanmi, L. A., Ogundipe, O. T., Ng, N. Q., Scoles, G. J., & Fatokun, C. A. (2007). Genetic diversity in yard-long bean (*Vigna unguiculata* subspecies *unguiculata* cv.-gr. *sesquipedalis*) as revealed by simple sequence repeat (SSR) markers. *Journal of Genetics and Breeding, 61*(1), 43–51. https://biblio.iita.org/documents/S07ArtOgunkanmiGeneticInthomDev.pdf-00f22584f43be4d50bc8bf3e978c4850.pdf

Owusu, E. Y., Amegbor, I. K., Darkwa, K., Oteng-Frimpong, R., & Sie, E. K. (2018). Gene action and combining ability studies for grain yield and its related traits in cowpea (*Vigna unguiculata*). *Cogent Food & Agriculture, 4*(1), 1519973. https://doi.org/10.1080/23311932.2018.1519973

Pessoa, A. M. dos S., Bertini, C. H. C. de M., Castro, É. B. de L., Freitas, L. M. de, & Sousa, T. R. M. de. (2024). Combining ability of cowpea genotypes for green grain production. *Revista Ceres, 71*, e71013. https://doi.org/10.1590/0034-737X2024710013

Schmidt, P., Hartung, J., Bennewitz, J., & Piepho, H.-P. (2019). Heritability in plant breeding on a genotype-difference basis. *Genetics, 212*(4), 991–1008. https://doi.org/10.1534/genetics.119.302134

Seck, F., Covarrubias-Pazaran, G., Gueye, T., & Bartholomé, J. (2023). Realized genetic gain in rice: Achievements from breeding programs. *Rice, 16*, Article 61. https://doi.org/10.1186/s12284-023-00677-6

Singh, B. B. (2005). Cowpea [*Vigna unguiculata* (L.) Walp.]. In R. J. Singh and P. P. Jauhar (Eds.), *Genetic resources, chromosome engineering, and crop improvement: Vol. 1. Grain legumes* (pp. 117–162). CRC Press. https://doi.org/10.1201/9780203489284-9

Sprague, G. F., & Tatum, L. A. (1942). General vs. specific combining ability in single crosses of corn. *Journal of the American Society of Agronomy, 34*(10), 923–932. https://doi.org/10.2134/agronj1942.00021962003400100008x

Tejaswini, V., Dey, S., Goud, B. G., Pujar, D. M., & Harshitha, D. K. (2025). Legumes: Breeding strategies and adaptive traits for drought tolerance. *International Journal of Environment and Climate Change, 15*(7), 278–298. https://doi.org/10.9734/ijecc/2025/v15i74929

Watanabe, I., Hakoyama, S., Terao, T., & Singh, B. B. (1997). Evaluation methods for drought tolerance of cowpea. In B. B. Singh, D. R. Mohan Raj, K. E. Dashiell, & L. E. N. Jackai (Eds.), *Advances in cowpea research* (pp. 141–146). International Institute of Tropical Agriculture and Japan International Research Center for Agricultural Sciences. https://cgspace.cgiar.org/items/309f3c2f-e700-43a7-91e1-ec32f1a78c61/full

Xiao, Y., Jiang, S., Cheng, Q., Wang, X., Yan, J., Zhang, R., Qiao, F., Ma, C., Luo, J., Li, W., Liu, H., Yang, W., Song, W., Meng, Y., Warburton, M. L., Zhao, J., Wang, X., & Yan, J. (2021). The genetic mechanism of heterosis utilization in maize improvement. *Genome Biology, 22*, Article 148. https://doi.org/10.1186/s13059-021-02370-7

Yadesa, L., Abebe, B., & Tafa, Z. (2022). Genetic variability, heritability, correlation analysis, genetic advance, and principal component analysis of grain yield and yield-related traits of quality protein maize (*Zea mays* L.) inbred lines adapted to the mid-altitude agroecology of Ethiopia. *EAS Journal of Nutrition and Food Sciences, 4*(1), 8–17. https://doi.org/10.36349/easjnfs.2022.v04i01.002

Yu, K., Wang, H., Liu, X., Xu, C., Li, Z., Xu, X., Liu, J., Wang, Z., & Xu, Y. (2020). Large-scale analysis of combining ability and heterosis for development of hybrid maize breeding strategies using diverse germplasm resources. *Frontiers in Plant Science, 11*, 660. https://doi.org/10.3389/fpls.2020.00660

Supplementary

Table S1. Mean performance of the ten hybrids and their parents under drought stress

Treatment	Yield T1	Yield T2	Biomass T1	Biomass T2
MA50 X NA11	1435.19	203.89	2623.89	1370.56
MA67 X NA60	1375.93	506.67	4123.33	1827.78
KK06	1014.44	56.61	1738.33	658.89
NA60	1080.74	199.44	790	620.56
KK06 X NA11	938.89	544.44	1678.89	295.56
MA50 X MA67	3220.37	562.5	5022.22	765
MA50 X NA20	490.74	100	197.78	659.44
NA20	311.3	147.78	2687.78	788.89
MA67	1563.33	110	567.22	257.78
NA11 X NA60	794.44	106.11	956.67	487.22
MA50 X NA60	781.48	538.89	1018.33	1690.56
MA50	730.74	354.17	1216.11	962.78
NA20 X NA60	1668.52	497.5	4481.11	515.56
MA67 X NA11	881.48	215	2457.22	537.22
NA11	1344.81	72.22	1364.44	1491.67
KK06 X MA67	811.11	385.56	4846.11	1192.22

Where KK = Kakamega accessions, NA = IITA accessions, MA = NGBK-KALRO-Muguga accessions

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