



Combining ability and gene action in Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes for agronomic traits

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Received: 14 December 2023 / Accepted: 2 April 2025 / Published online: 30 April 2025
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Abstract Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is a highly nutritious legume crop supporting sustainable food systems in arid and semi-arid agroecologies. However, modern varieties with high yield and desirable product profiles are yet to be bred in sub-Saharan Africa (SSA). Therefore, this study aimed to determine the combining ability effects and gene action in Bambara groundnut for yield and related traits to identify the best parents and derived families for breeding and genetic advancement. Ten complementary and contrasting parents were selected and crossed using a 10×10 half-diallel mating design, and 45 progenies developed. The progenies and parents were field evaluated using a 5×11 alpha lattice design with two replications in two contrasting

locations in South Africa. Data was collected on agronomic traits and subjected to statistical analyses to compute genetic parameters. The results revealed that the genotype×location interaction effect was significant ($P<0.001$) for the studied agronomic traits. The general combining ability (GCA) effects were significant ($P<0.05$) for the number of nodes per stem, number of secondary branches, number of pods per plant and seed length, while the specific combining ability (SCA) effects were significant ($P<0.05$) for yield per plant and assessed traits. A relatively lower Baker's ratio were recorded for most assessed traits at the F_1 , including grain yield per plant, indicating the preponderance of non-additive gene effects conditioning the traits. The parental lines such as ARC Bamb25, ARC Bamb8 and ARC Bamb55 recorded positive and desirable GCA effects for grain yield per plant and serve as suitable genetic resources for future breeding. The families ARC25×ARC8, ARC44×ARC9 and ARC6×ARC9 had desirable SCA effects for grain yield per plant. Therefore, the newly developed crosses with high yield potential are recommended for selection and genetic advancement using pedigree or pure line selection methods for variety registration and commercialisation.

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Keywords Bambara groundnut · Genetic analysis · General combining ability effect · Gene action · Specific combining ability effect

Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc.; $2n = 2x = 22$) is a nutrient-dense grain legume cultivated in sub-Saharan Africa (SSA) and Asia but largely under-researched and under-utilised. It is regarded as a complete food with a high potential to alleviate food and nutrition insecurity (Soumare et al. 2022). It can fix atmospheric nitrogen and improve soil fertility. In terms of total production, it is among the top three most vital legumes after groundnut (*Arachis hypogea* L.) and cowpea (*Vigna unguiculata* L.) (Mayes et al. 2019). Global production of Bambara groundnut is estimated at 240 000 tonnes per year from 406 911 hectares worldwide (FAO, 2023). Africa is the largest producer (239 607 tonnes per annum), while small quantities are produced in South-east Asia (e.g., Thailand and Indonesia), the United States of America, and Australia. West Africa is the centre of genetic diversity and the main Bambara groundnut production region in SSA, where Burkina Faso, Niger, and Cameroon are the leading producers, contributing to 74% of global production (FAO, 2023).

Bambara groundnut grains are nutrient-dense and ideal candidates to develop complete and value-added food products. The grains have balanced nutrient compositions including the following macro-nutrients (in mg per 100 g dry sample grain): nitrogen (17,000–26,000), phosphorus (81–563), potassium (1545–2200), and micro-nutrients such as magnesium (32–335), calcium (30–128), iron (2–9) and zinc (11–40) (Maphosa et al. 2022; Chelangat et al. 2023). Also, the grains contain carbohydrates (~ 72%), protein (~ 25%), fibre (~ 6.3%), and oil of ~ 7% (Ibny et al. 2019). Thus, the crop can contribute significantly to nutrition security, sustainable food systems and cash income through novel product development (De Valença et al. 2017).

Bambara groundnut enhances the productivity of agricultural soils by fixing atmospheric nitrogen through the symbiotic association with the micro-organism *Rhizobia* (Taffouo et al. 2010; Obayelu. 2016). Therefore, it is a suitable crop in regenerative agriculture and reduces the cost of inorganic fertilisers under smallholder farming systems. Crop rotation involving Bambara groundnut aids the restoration and maintenance of nitrogen supply in agricultural soils. Bambara groundnut is a relatively drought-tolerant

crop capable of withstanding long drought spells, making it a crop of choice in water-constrained environments (Mubaiwa et al. 2017).

The Bambara groundnut grain yield levels in SSA vary between 0.1 and 3.0 tonnes per hectare, with a mean of 0.85 tonnes per hectare (Azam-Ali et al. 2001; Mayes et al. 2019). The low yields are caused by biotic and abiotic stresses, poor farming practices and a lack of improved varieties (Hochholdinger and Baldauf 2018). Abiotic constraints include limited water availability, high temperatures, soil moisture stress, and infertile soils, which lead to limited yield potential (Ziervogel et al. 2014). Smallholder farmers, notably women, are the primary producers of the crop who lack modern production inputs. Farmers in SSA cultivate using traditional low-yielding genetically unimproved landrace varieties (Mbosso et al. 2020; Maphosa et al. 2022). Modern varieties with high yields and desirable product profiles are yet to be bred in sub-Saharan Africa. The lack of improved varieties has been reported widely as the main yield-limiting factor for sustainable and profitable crop production (Donkoh et al. 2016; Kendabie et al. 2020; Rafii et al. 2021). Consequently, low yields of Bambara groundnut render the crop less attractive and competitive for commercial production and product development.

There is a marked genetic variation for important agronomic traits (i.e., number of pods per plant, seeds per pod, days to maturity and yield potential) in Bambara groundnut genetic resources for pre-breeding and breeding (Beket et al. 2019; Uba et al. 2023). Pure line development is the common approach in strictly self-pollinating species, including Bambara groundnut, until effective hybridization methods are available for hybrid breeding to exploit heterosis (Odesola et al. 2023a, b). Bambara groundnut genetic diversity facilitates the identification of heterotic groups and the best parents for breeding. There is a need to identify the best combiner donor parents and progenies for genetic advancement and breeding of new generation varieties.

The concept of combining ability was proposed by Sprague and Tatum (1942). Combining ability analysis allows the selection of potential parents through progeny performance evaluation (Sawarkar et al. 2015). Good parental lines should be able to be used in a wide range of combinations with other lines to produce progenies that have high average performance. Combining abilities are distinguished as

general and specific combining ability effects. The general combining ability (GCA) effect refers to the average performance of a candidate line based on all its progenies generated from different cross combinations (Begna 2021). A line with a desirable GCA value for a trait of interest has a high potential to transmit the trait to its progenies and can be used in further crossing programs for varietal development. Conversely, the specific combining ability (SCA) effect is a cross or family's average performance (better or worse) than the mean of parental lines. The progenies that exhibit good SCA effects are primed for genetic advancement to develop stable breeding pure-line cultivars in self-pollinating crops. The ratios of GCA and SCA effects derived through combining ability analysis are used to deduce the gene action involved in the expression of quantitative characters (Mutari et al. 2022; Nassourou et al. 2022). The GCA effects are associated with additive gene action, while the SCA effects relate to non-additive gene action. Both genetic effects are essential in the development of breeding populations or in devising a suitable selection method (Viana and Matta. 2003). Different mating designs, including diallel are used to analyse combining ability effects and to deduce gene action controlling the inheritance of quantitative traits.

The diallel mating design is the most commonly used genetic design to determine the GCA of effects of parents and the SCA effects of progenies (Griffing 1956). It is a widely used design for self-pollinated species as the success rate for generating complete crosses is often lower (Singh 2007). It has been used in genetic analysis of traits of various legume crop

species such as cowpea (Tchiagam et al. 2011; Rodrigues et al. 2018; Owusu et al. 2020), soybean (El-Garhy et al. 2015, Kurasch et al. 2017, Adewale et al. 2023) and chickpea (Verma et al. 2010, Gaur et al. 2020; Lakhote et al. 2020). There is a lack of information on combining ability and genetic analyses of Bambara groundnut for agronomic traits. These could have partly contributed to limited breeding efforts to develop high-performing varieties with farmer-and-consumer-preferred traits for commercialisation in SSA. The combining ability effects of selected promising parents and their progeny should be assessed to create new breeding populations adapted to local growing conditions. Therefore, this study aimed to determine the combining ability effects and gene action in Bambara groundnut for yield and related traits to identify the best parents and derived families for breeding and genetic advancement.

Materials and methods

Plant materials

The study used 10 Bambara groundnut parental lines selected from preliminary evaluation trials based on agronomic, nutritional and genetic analysis using SNP markers (Majola et al. 2022). The names and attributes of the selected parental lines are presented in Table 1. The selected lines displayed high yield potential, better nutritional profiles and contrasting yield-related agronomic attributes, including maturity, pod length, stem thickness and seed colour.

Table 1 Description of Bambara groundnut genotypes used in the study

Genotype code	Genotype designation/Name	Source	Country of origin	Attributes
G6	ARC Bamb 6	ARC-VIMP	Botswana	Medium maturing, red seed colour, high Zn
G8	ARC Bamb 8	ARC-VIMP	South Africa	Early maturing, high yielding, high Fe and Ca
G9	ARC Bamb 9	ARC-VIMP	Botswana	High yield, thick stems, low grain tannins, high K
G25	ARC Bamb 25	ARC-VIMP	South Africa	Early maturing, high yielding, long pods, high Fe
G5	ARC Bamb 42	ARC-VIMP	South Africa	Large grain size, wide pods, high Zn and Ca
G7	ARC Bamb 44	ARC-VIMP	Botswana	Early maturing, mottled dry seeds, high Fe
G10	ARC Bamb 55	ARC-VIMP	South Africa	High yield, medium maturing, high P
G11	ARC Bamb 57	ARC-VIMP	Swaziland	Medium yield, quality fresh pods, high Mg
G12	ARC Bamb 66	ARC-VIMP	South Africa	Early maturing, cream seed colour, high Zn
G13	ARC Bamb 68	ARC-VIMP	South Africa	Wide pods, black seed colour, high Ca

ARC-VIMP = Agricultural Research Council – Vegetable, Industrial and Medicinal Plants Institute, Bamb = Bambara groundnut, Zn = Zinc, Fe = Iron, K = Potassium, P = Phosphorus Ca = Calcium.

Development of crosses

The 10 parental lines were established in 10 L capacity polyethylene pots, with two seeds planted per pot under a glasshouse environment at the Agricultural Research Council – Vegetable, Industrial and Medicinal Plants Institute, Pretoria, South Africa. A half-diallel mating design was used to generate 45 F_1 progenies. The parental lines were stagger planted at weekly intervals to facilitate emasculation and cross-pollination. The crossing procedure was done following the protocol developed by Morales and Singh (1991). Crosses were carried out manually and flowers were hand-emasculated to remove the anther sacs from the staminal column using fine forceps before the flowers opened up. Five flower buds per branch were emasculated, and pollen from a male donor was gently rubbed onto the stigma to facilitate cross-pollination. Pollination was conducted 24 h after emasculation to allow pollen receptiveness of the stigma. Both emasculation and pollination were carried out in the morning before 10:00 am. Each pollinated flower was tagged and labelled, indicating the parents involved in the cross and the crossing date. Since the success rate of crosses in Bambara groundnut is generally low (< 2%), multiple crosses were done to obtain sufficient seed for the field trials. At maturity, the seeds were harvested. After harvest, the seeds were stored under optimal conditions for later use.

Experimental sites and design

The 10 parental lines and 45 F_1 progenies were evaluated using a 5×11 alpha lattice design with two replications at two locations during the 2021/22 summer season (January 2021 to May 2022). The two locations were Brits (25.61° S 27.79° E) and Loskop (25.17° S 29.39° E). Brits is situated in the North-West province, while Loskop in the Mpumalanga province of South Africa. Brits' minimum and maximum temperatures were 18.6 and 28.9 °C, whereas Loskop experienced a minimum temperature of 18.0 °C and a

high temperature of 28.0 °C. The total rainfall at Brits was 629 mm and 497 mm at Loskop. The land was ploughed, disked, and rotavated at both sites to establish a fine seedbed. No basal or topdressing fertilisers were applied at ploughing and during plant growth. After land preparation, two seeds were hand-planted per hole. Each genotype was planted on a single-row plot of 1 m in length and with an intra-row spacing of 20 cm. Therefore, five plants were established for each genotype. The crop was established under rain-fed conditions with no supplementary irrigation. Standard Bambara groundnut production practices in South Africa were followed as outlined by Bambara groundnut descriptors of the International Plant Genetic Resources Institute (IPGRI, 2000). The fields were manually weeded where required.

Data collection

Data was collected on the following agronomic traits: number of days to 75% maturity (DM) determined as the number of days from sowing until when 75% of the pods in a plot turned brown, number of nodes per stem (NNS) were counted, number of secondary branches per stem (NSB) were counted at maturity, number of stems per plant (NSP) were counted at harvest, after shelling the average number of seeds were counted from 10 randomly selected and tagged plants, pod length (PodL) and pod width (PodW) were measured in centimetres at physiological maturity and recorded as the averages of 15 pods per genotype, stem thickness (ST) was measured using a Vernier calliper and recorded as an average of a random sample of five plants per plot, number of pods per plant (Npods) were counted at maturity and recorded as an average of 5 plants per plot, number of seeds per pod (NSPod) recorded as an average from a random sample of 10 pods from the plot, hundred seed weight (HSW) was determined as the weight of 100 randomly sampled seeds per plot after shelling, seed length (SL) and seed width (SW) recorded as averages of 10 random seeds per plot. SL was measured longitudinally, aiming the centre of the seed. SW was measured transversally from the hilum to the dorsal region in the central area of the seed. All the plants in a plot were harvested by digging the entire root system and pods from the ground. Grain yield per plant (YPP) was recorded as the average of grain weight

per plot divided by the number of harvested plants in a plot. Yield per plant was converted to kg ha⁻¹ using the following formula:

$$\left(\frac{\text{Plot weight(g)}}{\text{Plot area(m)}} * \frac{100 - 14}{100 - mc} \right) * 10000$$

where mc is moisture content measured at harvesting, which was 14% (Covert et al. 2017), and 10,000 is the conversion factor for a hectare.

Data analyses

Analysis of variance

Tests for normality and homogeneity of variance were conducted on the data from the individual locations prior to analysis of variance (ANOVA). The tests were conducted in GenStat® Version 18 (VSN International, Hemphstead, UK). ANOVA was conducted using Genstat to estimate statistical significance among genotypes and environments. The mean values were separated using Fisher's Least Significant Difference (LSD) test procedure at a 5% significance level. The following general linear model was used for the combined analysis of variance following Smith et al. (2005):

$$Y_{ijkl} = \mu + G_i + E_j + GE_{ij} + E(R)_{jk} + E[R(B)]_{jkl} + \varepsilon_{ijkl}$$

where Y_{ijkl} is the observed performance of the i th genotype grown in the j th location of k th replication within the l th incomplete block, μ is the grand mean, G_i is the effect of the i th genotype, E_j the effect of the j th location, GE_{ij} is the effect of the interactions of the i th genotype with the j th location; $E(R)_{jk}$ is the effect of the k th replication in the j th location, $E[R(B)]_{jkl}$ is the effect of the l th block within the k th replication in the j th location, and ε_{ijkl} is the residual effect associated with each Y_{ijkl} .

Combining ability analysis

Combining ability analysis was computed using the ImDiallel (Onofri et al. 2021) and Diallel AnalysisR (Yaseen and Eskridge 2020b, a) packages in R software version 4.2.1 (R Core Team 2022) following the random effects model II and method II (i.e., parents and

their progenies without reciprocals) according to Griffing (1956).

Combining ability analysis was carried out according to Kempthorne and Curnow (1961):

$$Y_{ij} = \mu + r_i + g_i + g_j + s_{ij} + \varepsilon_{ijk}$$

where Y_{ij} is the mean of the cross of between i th and j th parents, μ is the overall mean of the trial, r_i is the effects due to replication, g_i and g_j are the GCA effects of the i th and j th individuals, respectively, s_{ij} is the SCA effect for the cross between the i th and j th parents and ε_{ijk} is the residual error. The GCA effects were calculated as follows:

$$GCA = X_{ij} - \mu$$

where, X_{ij} is the mean of the i th parent across j crosses and μ is the overall mean.

The SCA effects were calculated as follows:

$$SCA = X_{ij} - (GCA_i + GCA_j + \mu)$$

where, X_{ij} is the mean of the cross between i th and j th parents, GCA_i and GCA_j are the GCA effects of the i th and j th parents and μ is the overall mean. The significance of GCA effects were tested based on the t-test in R software using the Diallel Analysis R package (Yaseen and Eskridge 2020b, a) as follows: $t = \frac{GCA}{se}$ and for SCA effects as $t = \frac{SCA}{se}$ Where se , is the standard error of the GCA or SCA estimates.

Estimates of genetic effects

The GCA and SCA variances were deduced from the analysis of variance, according to Agaba et al. (2017). The ratio of GCA to SCA variance ($\sigma^2_{gca}/(\sigma^2_{gca} + \sigma^2_{sca})$) was used to test the relative importance of additive versus non-additive gene action according to Baker (1978). Broad-sense heritability values were estimated as $H^2 = \frac{(\delta^2_{GCA} + \delta^2_{SCA})}{(\delta^2_{GCA} + \delta^2_{SCA} + \delta^2_e)}$ Where: $[\delta^2_{GCA} + \delta^2_{SCA}]$ = Total genetic effects, and $[\delta^2_{GCA} + \delta^2_{SCA} + \delta^2_e]$ = Phenotypic effects following Agaba et al. (2017).

Results

Analysis of variance and genotypic mean performance for agronomic traits

The ANOVA mean squares showed that location, genotype and genotype $\times$ location effects were significant ($P < 0.05$) for days to maturity (DM), number of nodes per stem (NNS), number of secondary branches (NSB), number of stems per plant (NSP), pod length (PodL), pod width (PodW), number of pods per plant (Npods), seed length (SL), seed width (SW) and yield per plant (YPP) (Table 2). Significant genotypic variation was observed for DM, NNS, NSB, PodL, PodW, Npods, SL, SW, hundred seed weight (HSW) and YPP. Location was significant for all the studied traits except HSW.

The mean performance for the assessed agronomic traits for the parental lines and their crosses across the two test locations are presented in Table 3. DM varied between 168 and 176 days for parental lines with ARC Bamb 9 recording fewer days to flowering (168 days) and ARC44 being late maturing (176 days). Crosses ARC66 $\times$ ARC44, ARC8 $\times$ ARC25, ARC55 $\times$ ARC44 were early maturing at 163, 164 and 165 days compared ARC8 $\times$ ARC55 and ARC8 $\times$ ARC66 that matured 177 and 178 days, respectively. The parents ARC Bamb 57 and ARC Bamb 68 recorded the highest NSB (≥ 20). Among the crosses, ARC8 $\times$ ARC25, ARC8 $\times$ ARC42, ARC8 $\times$ ARC44 recorded the maximum NSB of 26.

Pod length varied widely among the parental lines. The parent ARC Bamb 68 exhibited the longest pods (21.72 cm), followed by ARC Bamb 9 (20.44 cm) and ARC Bamb 57 (19.89 cm). Parental lines ARC Bamb 57 and ARC Bamb 68 also recorded the highest pod width of 15.34 cm and 14.92, respectively. The crosses ARC57 $\times$ ARC25, ARC68 $\times$ ARC25, ARC8 $\times$ ARC42 had long pods exceeding 22 cm. ARC57 $\times$ ARC25 had the highest pod width of 21.39 cm. Npods varied significantly from 83 to 170, which was generally lower for the crosses than the parental lines. Npods were recorded for ARC Bamb 44 (171), ARC Bamb 25 (124) and ARC Bamb 8 (121) parental lines. The maximum number of pods was 169 recorded for cross ARC6 $\times$ ARC57, while the minimum of 78 pods per plant was recorded for cross ARC66 $\times$ ARC44.

Table 2 Mean squares and significant tests for grain yield and yield components among Bambara groundnut genotypes evaluated across two locations

Sources of variation	Df	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
Location (Loc)	1	1364.4***	1400.4***	80.2*	1436.0***	72.3**	90.3***	46.5***	2418.0*	2826.8***	69 ns,0	500.8***	14.9*	2521.0*
Replication (Rep)	2	1663.1***	1745.9***	1105.4***	1117.6***	34.7*	453.1***	2.5*	14,960.0***	332.2 ns	9007.0***	505.7***	194.6***	11,393.0***
Block (Rep)	4	24.5 ns	130.7*	24.9 ns	0.9 ns	19.1 ns	11.0 ns	0.7 ns	2310.0***	265.9 ns	226.0 ns	142.3**	7.4*	576.0 ns
Genotype (Gen)	54	67.7***	201.7***	74.9***	11.3***	16.4**	16.3***	0.7 ns	2360.0***	113.6 ns	298.0 ns	130.3***	9.1***	1627.0***
Gen $\times$ Loc	54	76.7***	157.8***	91***	17.0***	18.5***	12.1***	0.6 ns	3289.0***	114.6 ns	273.0 ns	132.7***	8.4***	1284.0***
Residuals	214	34.5	43.9	13.90	5.8	9.8	5.2	0.6	420.0	145.8	334.0	33.8	3.0	554.0

Table 3 Mean values for agronomic traits among 45 F1 families and 10 parents of Bambara groundnut genotypes evaluated at Brits and Loskop in South Africa

Genotype	Traits												
	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
<i>Parents</i>													
ARC Bamb 6	174.00	21.17	18.83	9.50	19.43	12.80	0.77	110.17	16.15	51.03	10.49	8.56	97.41
ARC Bamb 8	171.17	25.78	19.78	8.17	17.51	13.83	0.65	121.17	16.17	51.65	12.49	8.66	99.03
ARC Bamb 9	168.67	20.17	14.00	7.17	20.44	12.13	0.63	112.50	21.25	49.75	10.95	8.81	95.52
ARC Bamb 25	171.33	21.05	15.00	8.33	19.08	15.34	0.46	123.67	22.00	57.26	15.03	9.40	109.55
ARC Bamb 42	174.00	46.67	19.17	8.05	18.03	13.98	0.52	83.00	13.17	51.07	10.64	8.64	95.22
ARC Bamb 44	176.33	26.83	16.17	8.83	17.65	14.07	0.49	170.67	17.17	47.09	12.03	8.50	78.72
ARC Bamb 55	169.83	27.17	15.33	8.00	17.14	14.27	0.71	100.83	18.33	45.84	12.56	10.43	122.33
ARC Bamb 57	172.83	29.00	20.17	8.33	19.89	14.92	0.68	102.67	24.67	48.76	10.34	8.95	104.92
ARC Bamb 68	172.00	25.70	21.12	9.00	21.72	14.67	0.75	116.00	26.33	54.11	15.32	9.44	108.25
ARC Bamb 66	169.00	26.00	16.17	8.00	18.93	13.12	0.55	93.83	15.17	58.00	11.00	8.84	89.40
<i>Crosses</i>													
ARC8 × ARC25	164.00	35.33	26.17	11.83	20.41	17.17	2.12	79.50	19.33	54.57	10.78	10.37	170.78
ARC9 × ARC44	172.60	33.08	16.83	8.67	19.60	14.50	0.65	90.67	21.33	56.14	13.35	10.57	133.25
ARC6 × ARC25	170.83	38.50	22.50	12.50	18.45	17.80	0.65	125.75	21.68	54.44	14.46	13.00	132.28
ARC9 × ARC6	170.00	20.50	14.50	7.50	18.68	13.31	0.72	111.17	26.00	66.41	11.88	9.52	129.34
ARC9 × ARC25	170.55	19.05	19.32	10.83	19.82	15.99	0.93	100.25	12.43	49.44	10.71	11.08	124.82
ARC44 × ARC25	167.50	29.08	20.67	11.17	20.70	12.51	0.85	102.00	24.50	50.41	11.39	10.97	122.80
ARC9 × ARC55	169.50	20.83	16.42	8.00	20.07	13.48	0.64	121.17	18.73	50.24	11.56	8.18	121.02
ARC8 × ARC6	177.33	26.33	16.05	9.08	20.48	14.28	0.59	132.00	19.75	55.64	14.70	12.38	116.45
ARC9 × ARC8	176.17	21.67	15.67	10.83	19.00	13.63	0.68	135.50	23.50	48.24	13.46	11.49	113.27
ARC68 × ARC55	169.17	29.33	19.83	8.83	18.64	15.13	0.76	116.50	23.50	66.09	11.71	8.87	113.23
ARC55 × ARC44	165.50	26.50	13.75	7.33	18.73	14.51	0.75	104.50	22.83	50.43	10.80	10.20	112.67
ARC8 × ARC55	177.33	26.83	20.00	8.83	21.82	15.55	0.41	90.17	13.50	50.47	12.41	10.80	112.18
ARC42 × ARC25	171.30	24.27	15.03	7.83	20.81	18.34	0.78	97.17	17.33	50.44	10.89	10.14	110.80
ARC6 × ARC55	171.00	27.83	18.17	7.17	19.26	13.61	0.52	89.92	14.42	44.61	11.36	9.83	108.28
ARC8 × ARC66	178.00	22.17	19.83	8.67	22.22	15.16	0.44	132.50	19.50	55.49	9.44	9.59	107.95
ARC57 × ARC55	172.83	17.17	18.33	8.33	20.45	15.10	0.42	113.00	22.33	59.75	13.75	9.36	105.22
ARC66 × ARC57	169.33	23.00	14.83	9.67	18.10	13.45	0.59	101.50	12.75	55.59	11.11	9.32	104.95
ARC66 × ARC55	174.83	30.83	22.17	8.17	19.34	15.15	0.58	121.17	17.00	57.74	11.94	9.40	103.07
ARC6 × ARC42	167.33	29.47	15.92	8.05	17.54	13.50	0.51	94.38	26.33	51.48	11.07	9.66	102.88
ARC6 × ARC44	168.67	20.67	17.37	8.50	19.35	15.92	0.37	105.25	15.00	48.98	12.87	8.98	102.78
ARC8 × ARC44	174.00	19.33	25.93	7.75	19.58	16.86	0.82	123.95	19.17	57.70	14.24	9.84	102.28
ARC8 × ARC42	175.50	24.00	26.00	11.33	22.42	15.24	0.58	96.50	16.00	57.09	14.05	9.81	101.68
ARC66 × ARC25	169.33	25.70	22.77	8.33	19.64	14.23	0.68	102.50	30.10	84.14	12.49	10.97	101.51
ARC8 × ARC68	171.83	27.70	20.27	7.83	20.60	17.09	0.73	116.67	19.17	61.72	12.38	10.08	100.62
ARC55 × ARC25	168.08	28.23	22.30	8.13	19.85	13.15	0.93	115.17	17.05	51.02	13.54	10.58	99.90
ARC9 × ARC57	170.67	21.83	17.33	8.33	17.90	15.27	0.77	112.37	25.50	49.64	11.31	8.46	98.33
ARC68 × ARC6	170.00	21.67	14.75	8.67	22.17	13.60	0.42	122.67	21.00	70.48	11.03	9.49	97.70
ARC66 × ARC42	167.17	25.67	16.50	7.00	18.97	14.67	0.57	115.00	24.67	61.66	11.27	9.07	97.53
ARC57 × ARC44	167.17	27.50	15.17	8.50	19.23	14.76	0.57	127.67	18.17	55.78	11.89	9.35	96.80
ARC68 × ARC57	170.17	22.50	18.67	7.83	17.39	15.43	0.64	110.67	20.83	48.54	10.17	8.56	96.47
ARC8 × ARC57	173.50	34.00	17.50	7.83	18.06	13.08	0.73	162.33	13.17	45.12	10.01	5.63	96.20
ARC66 × ARC6	170.17	23.83	13.50	7.50	17.56	12.66	0.56	125.33	20.83	59.29	12.14	9.45	96.10

Table 3 (continued)

Genotype	Traits												
	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
ARC44 × ARC42	171.17	25.83	18.83	8.33	19.65	14.19	0.35	111.50	23.00	50.81	10.67	8.69	95.33
ARC6 × ARC57	172.67	18.83	13.33	7.83	21.91	14.64	0.60	169.00	16.25	56.83	11.48	9.33	94.93
ARC57 × ARC42	167.50	41.50	13.50	7.33	16.37	13.61	0.37	98.25	15.67	44.50	11.28	12.85	93.38
ARC55 × ARC42	171.50	20.17	17.78	9.17	19.01	13.88	0.59	146.83	10.83	45.41	12.31	8.66	91.63
ARC9 × ARC66	175.83	24.17	16.67	8.50	18.05	16.58	0.59	156.33	15.67	53.01	11.17	10.21	90.44
ARC68 × ARC66	168.67	21.07	21.23	8.33	17.32	15.18	0.56	107.33	15.67	52.22	10.20	8.72	89.92
ARC68 × ARC25	168.00	23.50	25.00	10.17	23.35	17.27	0.76	90.92	15.75	53.89	12.44	10.99	88.70
ARC68 × ARC42	165.83	24.67	16.67	7.17	21.28	16.14	0.49	106.20	20.05	54.79	12.31	10.90	87.40
ARC66 × ARC44	163.83	14.83	13.67	8.33	21.37	14.06	0.66	78.50	16.00	46.37	12.26	9.20	84.53
ARC57 × ARC25	170.50	26.92	25.17	13.50	23.91	21.39	0.88	122.67	12.50	58.67	11.45	9.49	83.10
ARC68 × ARC44	175.00	20.67	23.83	7.83	18.76	15.76	0.57	123.33	14.50	44.29	12.13	10.31	80.46
ARC9 × ARC42	175.83	23.00	21.50	9.00	17.56	12.93	2.43	108.50	21.33	47.16	14.34	11.45	78.94
ARC9 × ARC68	169.83	23.33	17.00	9.00	20.23	16.06	0.58	107.00	17.00	53.91	13.31	8.82	69.46
Mean	171.03	25.50	20.33	8.70	19.55	14.82	0.68	113.74	18.95	53.73	12.55	9.72	102.94
CV (%)	3.47	25.71	20.33	23.87	13.37	15.33	113.17	17.79	64.11	25.76	46.60	17.87	22.86
LSD (5%)	85.30	10.60	29.50	95.60	1.40	1.30	0.90	3.60	1.40	2.70	0.50	1.30	7.20

For HSW, parental lines ARC Bamb 68 and ARC Bamb 25 recorded heavier seeds exceeding 50 g. Among the crosses, ARC66 × ARC25, ARC68 × ARC6 and ARC9 × ARC6 recorded the mean HSW of 84.14 g, 70.48 g and 66.41 g, respectively. The yield per plant varied from 78.72 to 122.33 kg ha⁻¹ across parents and crosses. Parental lines ARC Bamb 55, ARC Bamb 25 and ARC Bamb 68 were the top-yielding lines with mean values of 122.33, 109.55 and 108.25 kg ha⁻¹, respectively. The lowest-yielding parent was ARC Bamb 44, recording grain yield of 78.72 kg ha⁻¹. In general, the mean yield of the progenies was higher than the parental genotypes, with only ARC68 × ARC44 (80.46 kg ha⁻¹) and ARC9 × ARC42 (78.94 kg ha⁻¹) having similar or lower yields than the lowest-yielding parental genotypes. Cross ARC8 × ARC25 had the highest YPP (170.78 kg ha⁻¹), followed by ARC9 × ARC44 (133.25 kg ha⁻¹) and ARC6 × ARC25 (132.28 kg ha⁻¹).

DF = degrees of freedom, DM = days to 75% maturity, NNS = Number of nodes per stem, NSB = number of secondary branches per stem, NSP = number of stems per plant, PodL = Pod length (cm), PodW = Pod width (cm), ST = Stem thickness (1/100 mm), Npods = Number of pods per plant, NSPod = Number of seeds per pod, HSW = Hundred seed weight (g/100

seed), SL = Seed length (cm), SW = Seed width (cm) and YPP =

yield per plant (kg ha⁻¹). *, ** and *** denote significant at 0.05, 0.01 and 0.001 probability levels, respectively. ns = Non-significant.

DM = days to 75% maturity, NNS = Number of nodes per stem, NSB = number of secondary branches per stem, NSP = number of stems per plant, PodL = Pod length (cm), PodW = Pod width (cm), ST = Stem thickness (1/100 mm), Npods = Number of pods per plant, NSPod = Number of seeds per pod, HSW = Hundred seed weight (g/100 seed), SL = Seed length (cm), SW = Seed width (cm) and YPP = yield per plant (kg ha⁻¹), ARC-VIMP = Agricultural Research Council, Bamb = Bambara, CV = coefficient of variation, LSD = least significant difference.

Analysis of variance for combining ability effects for agronomic traits

Analysis of variance showing GCA and SCA mean squares for the studied agronomic traits amongst Bambara groundnut parental lines and progenies are summarized in Table 4. Location × GCA interaction effects were significant for all the traits except number of stems per plant (NSP), days to 75% maturity

Table 4 Combining ability analysis of variance for agronomic traits of 45 Bambara groundnut families evaluated at Brits and Loskop in South Africa

Source of variation	DF	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
Location (Loc)	1	1364.4***	1400.4***	80.2*	1436.0***	72.3**	90.3***	46.4***	2418.0*	2826.8***	69.0 ns	500.8***	14.9*	2521.0*
Replication (Rep)	2	1663.1***	1745.9***	1105.4***	117.6***	34.7	453.1***	2.5*	14,960.0***	332.2 ns	9007.0***	505.7***	194.6***	11,393.0***
Block	4	24.5 ns	130.7*	24.9 ns	0.9 ns	19.1 ns	11.0 ns	0.6 ns	2310.0***	265.9 ns	226.0 ns	142.3**	7.3*	576.0 ns
SCA	45	74.3***	177.0***	82.9***	13.1***	17.3**	18.5***	0.8 ns	2201.0***	112.2 ns	341.0 ns	24.2 ns	10.5***	1770.0***
GCA	9	34.5 ns	325.6***	35.3**	2.5 ns	11.7 ns	5.3 ns	0.1 ns	3155.0***	120.8 ns	83.0 ns	660.6***	1.8 ns	909.0 ns
Loc x SCA	45	88.0***	132.3***	97.8***	20.2***	18.4**	11.4***	0.7 ns	2988.0***	115.7 ns	300.0 ns	22.6 ns	9.3***	1305.0***
Loc x GCA	9	19.9 ns	285.4***	57.1***	1.1 ns	18.4 ns	16.0**	0.1 ns	4793.0***	109.0 ns	139.0 ns	682.9***	3.5 ns	1183.0*
Residuals	214	34.50	43.90	13.90	5.80	9.80	5.20	0.61	420.0	145.80	334.00	33.80	3.00	554.00
σ^2_{sca}		5.81	68.64	16.93	0.96	1.79	3.02	0.03	270.90	3.12	43.15	12.65	2.10	410.73
σ^2_{gea}		0.76	18.30	5.67	0.49	0.67	1.63	0.01	300.20	1.01	29.97	65.02	0.86	127.30
Residual		54.24	79.96	37.25	8.62	11.87	9.76	0.62	1100.50	138.00	369.50	51.36	5.42	779.99
Baker's ratio		0.12	0.21	0.25	0.34	0.27	0.35	0.26	0.53	0.24	0.41	0.84	0.29	0.24
Heritability (%)		10.81	52.09	37.76	14.42	17.15	32.27	5.76	34.16	2.91	16.52	60.20	35.34	40.82

(DM), pod length (PodL), stem thickness (ST), number of seeds per pod (NSPod), hundred seed weight (HSW) and seed width (SW). Similarly, location $\times$ SCA effects were significant for most traits except for ST, NSPod, HSW and seed length (SL). There were significant ($P < 0.05$) GCA effects for number of nodes per stem (NNS), number of secondary branches (NSB), NPods and SL. Significant ($P \leq 0.05$) SCA effects were observed for most traits except for ST, NSPod, HSW and SL. Broad-sense heritability varied from 2.91% to 60.20% across the studied traits. SL recorded the highest heritability estimate (60.20%), followed by NNS (52.09%) and YPP (40.82%), whereas NSPod showed the lowest heritability (2.91%).

General combining ability effects of parental lines for agronomic traits

The GCA effects of the parents for the studied agronomic traits across the test locations are presented in Table 5. The parental lines ARC Bamb 25 and ARC Bamb 8 recorded negative and desirable GCA effect for DM. Significant and positive GCA effects for NSP were recorded for ARC Bamb 25, ARC Bamb 57, ARC Bamb 68 and ARC Bamb 8. Significant and desirable GCA effects for NNS, NSB, NSP PodL ST and YPP were computed for ARC Bamb 25. Parental line ARC Bamb 57 and ARC Bamb 8 exhibited significant and positive GCA effects for NSP, PodL, NPods and YPP. Significant and desirable GCA effects were recorded for HSW, YPP, SL and SW by ARC Bamb 66 and ARC Bamb 68. Parental lines ARC Bamb 25, ARC Bamb 55, ARC Bamb 57, ARC Bamb 66, ARC Bamb 68 and ARC Bamb 8 were the best combiners for YPP, recording high and positive GCA effects.

DM = days to 75% maturity, NNS = Number of nodes per stem, NSB = number of secondary branches per stem, NSP = number of stems per plant, PodL = Pod length (cm), PodW = Pod width (cm), ST = Stem thickness (1/100 mm), NPods = Number of pods per plant, NSPod = Number of seeds per pod, HSW = Hundred seed weight (g/100 seed), SL = Seed length (cm), SW = Seed width (cm) and YPP = yield per plant (kg ha^{-1}), SCA = specific combining ability, GCA = general combining ability, Loc = location, σ^2_{sca} = specific combining ability variance, σ^2_{gca}

Table 5 General combining ability effects for agronomic traits in Bambara groundnut parental lines evaluated at Brits and Loskop in South Africa

Parents	DM	NNS	NSB	NSP	PodL	PodW	ST	NPods	NSPod	HSW	SL	SW	YPP
ARC Bamb 25	- 1.79*	1.81*	2.86***	1.52***	0.99**	1.41***	0.21*	- 7.81**	0.33 ns	2.47 ns	0.01 ns	0.90***	11.19***
ARC Bamb 42	- 0.22 ns	3.17***	- 0.43 ns	- 0.41 ns	- 0.44 ns	- 0.26 ns	0.02 ns	- 8.03**	- 0.09 ns	- 2.51 ns	- 0.41 ns	0.19 ns	- 7.75**
ARC Bamb 44	- 0.76 ns	- 0.92 ns	- 0.30 ns	- 0.21 ns	- 0.14 ns	- 0.19 ns	- 0.08 ns	0.03 ns	0.23 ns	- 3.15 ns	- 0.13 ns	- 0.13 ns	- 2.26 ns
ARC Bamb 55	0.01 ns	0.13 ns	- 0.11 ns	- 0.54*	- 0.17 ns	- 0.52 ns	- 0.05 ns	- 1.84 ns	- 1.08 ns	- 1.79 ns	- 0.10 ns	- 0.16 ns	5.72*
ARC Bamb 57	- 0.22 ns	0.87 ns	- 1.12*	0.23*	0.28*	0.25 ns	- 0.06 ns	8.24**	- 0.75 ns	- 1.64 ns	- 1.01 ns	- 0.66**	5.80*
ARC Bamb 6	0.25 ns	- 0.47 ns	- 2.03***	- 0.11 ns	- 0.12 ns	- 0.69*	- 0.11 ns	4.79 ns	0.80 ns	1.96 ns	- 0.15 ns	0.22 ns	4.58 ns
ARC Bamb 66	- 0.32 ns	- 1.62*	- 0.78 ns	- 0.49 ns	- 0.45 ns	- 0.48 ns	- 0.11 ns	- 0.36 ns	- 0.20 ns	4.39*	0.19*	0.31*	6.69*
ARC Bamb 68	- 0.89 ns	- 1.34 ns	1.31**	0.27*	0.53 ns	0.72*	- 0.06 ns	- 2.04 ns	0.44 ns	2.04*	2.80***	0.17*	10.01**
ARC Bamb 8	2.94***	0.96 ns	2.19***	0.47*	0.60*	0.28 ns	0.08 ns	5.25*	- 1.01 ns	- 0.18 ns	0.09 ns	0.07 ns	8.81**
ARC Bamb 9	1.02 ns	- 2.59**	- 1.59**	0.04 ns	- 0.47 ns	- 0.51 ns	0.17 ns	1.77 ns	1.33 ns	- 1.56 ns	- 0.09 ns	0.06 ns	2.20 ns

= general combining ability variance. *, ** and *** denote significant at 0.05, 0.01 and 0.001 probability levels, respectively. ns = Non-significant.

DM = days to 75% maturity, NNS = Number of nodes per stem, NSB = number of secondary branches per stem, NSP = number of stems per plant, PodL = Pod length (cm), PodW = Pod width (cm), ST = Stem thickness (1/100 mm), Npods = Number of pods per plant, NSPod = Number of seeds per pod, HSW = Hundred seed weight (g/100 seed), SL = Seed length (cm), SW = Seed width (cm) and YPP = yield per plant (kg ha^{-1}). ARC-VIMP = Agricultural Research Council, Bamb = Bambara, *, ** and *** Significant at 0.05, 0.01 and 0.001 probability level, respectively. ns = Non-significant,

Specific combining ability effects of crosses for agronomic traits

Table 6 presented the SCA effects for agronomic traits of 45 Bambara groundnut crosses evaluated across two locations. Crosses ARC25 $\times$ ARC8, ARC44 $\times$ ARC55 and ARC44 $\times$ ARC66 had significant and negative SCA effects for DM, which were in the desirable direction. Three crosses, namely ARC42 $\times$ ARC57, ARC25 $\times$ ARC8 and ARC44 $\times$ ARC9 exhibited the highest and positive SCA effects for NNS. For branching capacity, there were seven crosses that exhibited positive and significant effects for NSB. Crosses including ARC25 $\times$ ARC57, ARC57 $\times$ ARC6, and ARC42 $\times$ ARC8 exhibited positive GCA effects for PodL. Only one cross ARC25 $\times$ ARC66 recorded positive and significant SCA effects for NSPods. Significant and positive SCA effects for YPP were recorded for three crosses: ARC25 $\times$ ARC8, ARC44 $\times$ ARC9 and ARC6 $\times$ ARC9. Crosses ARC25 $\times$ ARC55, ARC25 $\times$ ARC57, ARC25 $\times$ ARC9, ARC42 $\times$ ARC9, and ARC68 $\times$ ARC9 had undesirably high and negative SCA effects for YPP.

DM = days to 75% maturity, NNS = Number of nodes per stem, NSB = number of secondary branches per plant, NSP = number of stems per plant, PodL = Pod length, PodW = Pod width, ST = Stem thickness (1/100 mm), Npods = Number of pods per plant, NSPod = Number of seeds per pod, HSW = Hundred seed weight (g), SL = Seed length, SW = Seed width and YPP = yield per plant. ARC-VIMP

= Agricultural Research Council, *, ** and *** denote significant at 0.05, 0.01 and 0.001 probability levels, respectively. ns = non-significant.

Discussion

Bambara groundnut has unique adaptations to drought and low-input agricultural systems. Its excellent nutrient profile makes it an ideal candidate for developing various food products. In continental Africa, the crop is cultivated using genetically diverse landrace varieties, which are low-yielding (< 2.3 ton/ha), thus limiting the crop's large-scale production and commercial value. There is a need for dedicated breeding to develop high-performing Bambara groundnut varieties with farmer-and-consumer preferred traits for adoption by growers and industry.

The present study determined the combining ability effects and gene action controlling yield and related traits in Bambara groundnut to identify superior genotypes as parents and to develop breeding populations for selection and genetic advancement. The presently assessed populations showed marked genetic variation for agronomic traits, including days to maturity, pod length, pod width and grain yield (Table 2). These indicated the selected parents and the new crosses could be useful for breeding, targeting high-yield potential and desirable agronomic traits. The early maturing parental lines and crosses are useful in developing drought-escape varieties for cultivation in short-season production environments. Early maturing crosses ARC8 $\times$ ARC25, ARC68 $\times$ ARC42, ARC66 $\times$ ARC44 and ARC55 $\times$ ARC44 (Table 3) are selected as best recombinants to enhance early flowering and maturity. Farmers in sub-Saharan Africa are challenged by increasingly short rainy seasons due to climate change (Onyango and Nzengya 2023). Developing genotypes that can escape terminal drought stress would increase the productivity of Bambara groundnut in drought-prone agroecologies.

Developing varieties with high grain yield potential is a desirable trait for increasing the productivity of Bambara groundnut. Also, these crosses must incorporate other vital characteristics such as secondary branching, earliness and seed quality to satisfy different market segments. Crosses ARC8 $\times$ ARC25 and ARC6 $\times$ ARC25 exhibited higher grain yield potential than their parental lines (Table 3). These

Table 6 Specific combining ability effects for grain yield and yield-related traits in 45 newly developed hybrids of Bambara groundnut evaluated at Brits and Loskop in South Africa

Crosses	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
ARC25 × ARC42	2.38 ns	-6.06*	-5.92***	-2.01*	0.65 ns	2.28*	-0.15 ns	-0.75 ns	-1.83 ns	-3.46 ns	-1.01 ns	-0.75 ns	4.12 ns
ARC25 × ARC44	-0.87 ns	2.84 ns	-0.42 ns	1.11 ns	0.24 ns	-3.61***	0.02 ns	-3.99 ns	5.00 ns	-2.85 ns	-0.79 ns	0.40 ns	10.64 ns
ARC25 × ARC55	-1.07 ns	0.93 ns	1.02 ns	-1.58*	-0.56 ns	-2.64**	0.08 ns	11.05 ns	-1.13 ns	-3.61 ns	1.32 ns	0.03 ns	-20.24*
ARC25 × ARC57	1.58 ns	-1.11 ns	4.89**	3.22***	3.60***	4.81***	0.03 ns	8.46 ns	-6.01 ns	3.88 ns	0.15 ns	-0.54 ns	-25.52**
ARC25 × ARC6	1.43 ns	11.81***	3.13*	2.34**	-2.02*	2.17*	-0.13 ns	14.99 ns	1.60 ns	-3.95 ns	2.29 ns	2.07**	13.27 ns
ARC25 × ARC66	0.51 ns	0.16 ns	2.16 ns	-1.43 ns	-0.50	-1.60 ns	-0.11 ns	-3.08 ns	11.03*	23.31***	1.16 ns	0.58 ns	-6.22 ns
ARC25 × ARC68	-0.25 ns	-2.32 ns	2.29 ns	0.17 ns	2.21*	0.22 ns	-0.07 ns	-13.00 ns	-3.96 ns	-4.58 ns	-2.67 ns	0.47 ns	-15.71 ns
ARC25 × ARC8	-8.08***	7.20**	2.57 ns	1.09 ns	-0.78 ns	0.56 ns	1.13***	-31.71***	1.07 ns	-1.66 ns	-1.63 ns	-0.40 ns	47.54***
ARC25 × ARC9	0.38 ns	-5.52*	-0.47 ns	0.52 ns	-0.31 ns	0.19 ns	-0.14 ns	-7.48 ns	-8.17 ns	-5.42 ns	-1.51 ns	0.31 ns	8.18 ns
ARC42 × ARC44	1.21 ns	-1.77 ns	1.04 ns	0.22 ns	0.62 ns	-0.26 ns	-0.28 ns	5.73 ns	3.93 ns	2.52 ns	-1.07 ns	-1.16 ns	2.12 ns
ARC42 × ARC55	0.77 ns	-8.49**	-0.19 ns	1.38 ns	0.02 ns	-0.24 ns	-0.07 ns	42.94***	-6.92 ns	-4.23 ns	0.52 ns	-1.16 ns	-9.56 ns
ARC42 × ARC57	-2.98 ns	12.1***	-3.46*	-1.00 ns	-2.50*	-1.29 ns	-0.28 ns	-15.72*	-2.41 ns	-5.29 ns	0.41 ns	3.52***	3.70 ns
ARC42 × ARC6	-3.63 ns	1.41 ns	-0.14 ns	-0.16 ns	-1.49 ns	-0.45 ns	-0.09 ns	-16.14*	6.68 ns	-1.91 ns	-0.66 ns	-0.54 ns	2.81 ns
ARC42 × ARC66	-3.22 ns	-1.23 ns	-0.80 ns	-0.83 ns	0.26 ns	0.50 ns	-0.03 ns	9.63 ns	6.02 ns	5.82 ns	0.38 ns	-0.59 ns	8.74 ns
ARC42 × ARC68	-3.98 ns	-2.51 ns	-2.73 ns	-0.88 ns	1.58 ns	0.77 ns	-0.16 ns	2.50 ns	0.76 ns	1.30 ns	-2.37 ns	1.09 ns	1.93 ns
ARC42 × ARC8	1.84 ns	-5.48*	5.71***	2.53**	2.65**	0.30 ns	-0.22 ns	-14.49 ns	-1.82 ns	5.83 ns	2.07 ns	-0.24 ns	-2.61 ns
ARC42 × ARC9	4.09 ns	-2.93 ns	5.00**	0.63 ns	-1.12 ns	-1.19 ns	1.54***	0.99 ns	1.15 ns	-2.71 ns	2.55 ns	1.40*	-18.75*

Table 6 (continued)

Crosses	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
ARC44 × ARC55	− 4.69*	1.93 ns	− 4.35**	− 0.64 ns	− 0.55 ns	0.32 ns	0.19 ns	− 7.45 ns	4.75 ns	1.42 ns	− 1.26 ns	0.70 ns	5.98 ns
ARC44 × ARC57	− 2.78 ns	2.19 ns	− 1.93 ns	− 0.03 ns	0.06 ns	− 0.20 ns	0.02 ns	5.62 ns	− 0.24 ns	6.61 ns	0.74 ns	0.35 ns	1.63 ns
ARC44 × ARC6	− 1.76 ns	− 3.29 ns	1.17 ns	0.08 ns	0.01 ns	1.9*ns	− 0.11 ns	− 13.34 ns	− 4.97 ns	− 3.78 ns	0.85 ns	− 0.90 ns	− 2.76 ns
ARC44 × ARC66	− 6.01*	− − 7.97**	− 3.76*	0.29 ns	2.37*	− 0.17 ns	0.16 ns	− 34.93***	− 2.96 ns	− 8.82 ns	1.09 ns	− 0.14 ns	− 9.74 ns
ARC44 × ARC68	5.71*	− 2.42 ns	4.29**	− 0.41 ns	− 1.23 ns	0.31 ns	0.02 ns	11.57 ns	− 5.11 ns	− 8.55 ns	− 2.83 ns	0.82 ns	− 10.48 ns
ARC44 × ARC8	0.88 ns	− 6.06*	5.51***	− 1.25 ns	− 0.48 ns	1.86*	0.12 ns	4.88	1.01 ns	7.09 ns	1.98 ns	0.11 ns	− 7.49 ns
ARC44 × ARC9	1.40 ns	11.24***	0.21 ns	0.09 ns	0.61 ns	0.30 ns	− 0.13 ns	− 24.91**	0.82 ns	6.90 ns	1.28 ns	0.84 ns	30.08**
ARC55 × ARC57	2.10 ns	− 9.19***	1.04 ns	0.12 ns	1.30 ns	0.46 ns	− 0.14 ns	− 7.16 ns	5.23 ns	9.22 ns	2.57 ns	0.39 ns	2.06 ns
ARC55 × ARC6	− 0.21 ns	2.81 ns	1.78 ns	− 0.91 ns	− 0.04 ns	− 0.07 ns	0.01 ns	− 26.80**	− 4.24 ns	− 9.51 ns	− 0.67 ns	− 0.02 ns	− 5.26 ns
ARC55 × ARC66	4.2 ns	6.97**	4.54**	0.46 ns	0.36 ns	1.24 ns	0.06 ns	9.61 ns	− 0.65 ns	1.19 ns	0.74 ns	0.08 ns	0.80 ns
ARC55 × ARC68	− 0.89 ns	5.18*	0.10 ns	0.91 ns	− 1.32 ns	0.02 ns	0.19 ns	6.6ns1	5.20 ns	11.88*	− 3.28 ns	− 0.58 ns	14.29 ns
ARC55 × ARC8	3.43 ns	0.38 ns	− 0.60 ns	0.16 ns	1.79 ns	0.88 ns	− 0.30 ns	− 27.01**	− 3.34 ns	− 1.49 ns	0.11 ns	1.10 ns	− 5.58 ns
ARC55 × ARC9	− 2.48 ns	− 2.06 ns	− 0.39 ns	− 0.23 ns	1.11 ns	− 0.38 ns	− 0.16 ns	7.46 ns	− 0.46 ns	− 0.35 ns	− 0.53 ns	− − 1.51*	9.85 ns
ARC57 × ARC6	1.69 ns	− 6.91**	2.03*	− 0.80 ns	2.71**	0.16 ns	0.09 ns	42.19***	− 2.73 ns	2.55 ns	0.35 ns	− − 0.02 ns	− 7.08 ns
ARC57 × ARC66	− 1.05 ns	− 1.59 ns	− 1.77 ns	1.40 ns	− 0.76 ns	− 1.23 ns	0.07 ns	− 20.14*	− 5.23 ns	− 1.12 ns	0.82 ns	0.50 ns	14.21 ns
ARC57 × ARC68	0.34 ns	− 2.38 ns	− 0.04 ns	− 0.64 ns	− 2.46*	− 0.46 ns	0.07 ns	− 9.30 ns	2.20 ns	− 5.82 ns	− 3.91 ns	− 0.39 ns	9.04 ns
ARC57 × ARC8	− 0.15 ns	6.81**	− 2.09 ns	− 1.39 ns	− 1.86 ns	− 2.36**	0.01 ns	35.06***	− 4.00 ns	− 7.00 ns	− 1.36 ns	− 3.56***	− 10.04 ns
ARC57 × ARC9	− 1.07 ns	− 1.80 ns	1.53 ns	− 0.45 ns	− 0.94 ns	0.62 ns	− 0.02 ns	− 11.42 ns	5.97 ns	− 1.11 ns	0.12 ns	− 0.73 ns	− 1.31 ns

Table 6 (continued)

Crosses	DM	NNS	NSB	NSP	PodL	PodW	ST	Npods	NSPod	HSW	SL	SW	YPP
ARC6 × ARC66	− 0.70 ns	0.58 ns	− 2.20 ns	− 0.63 ns	− 1.46 ns	− 1.07 ns	0.10 ns	7.13 ns	1.29 ns	− 1.02 ns	0.99 ns	− 0.24 ns	− 5.02 ns
ARC6 × ARC68	− 0.30 ns	− 1.87 ns	− 3.05*	0.31 ns	2.14*	− 1.33 ns	− 0.09 ns	6.14 ns	0.81 ns	12.52*	− 3.91 ns	− 0.35 ns	− 0.10 ns
ARC6 × ARC8	3.19 ns	0.49 ns	− 2.63 ns	− 0.02 ns	0.39 ns	− 0.21 ns	− 0.06 ns	8.17 ns	1.01 ns	− 0.08 ns	2.45 ns	2.29**	− − 0.17 ns
ARC6 × ARC9	− 2.22 ns	− 1.79 ns	− 0.39 ns	− 1.17 ns	− 0.32 ns	− 0.37 ns	− 0.02 ns	− 9.17 ns	4.92 ns	12.05*	− 0.17 ns	− 0.56 ns	19.31*
ARC66 × ARC68	− 1.05 ns	− 1.32 ns	2.18 ns	0.35 ns	− 2.36*	0.02 ns	0.04 ns	− 4.02 ns	− 3.51 ns	− 8.17 ns	− 3.90 ns	− 0.58 ns	3.38 ns
ARC66 × ARC8	4.44 ns	− 2.52 ns	− 0.09 ns	− 0.05 ns	2.47*	0.45 ns	− 0.22 ns	13.84 ns	1.77 ns	− 2.67 ns	− 1.95 ns	0.04 ns	2.59 ns
ARC66 × ARC9	4.19 ns	3.03 ns	0.53 ns	0.20 ns	− − 0.62 ns	2.67**	− 0.15 ns	41.15***	− 4.40 ns	− 3.77 ns	− 0.04 ns	0.66 ns	− 8.30 ns
ARC68 × ARC8	− 1.15 ns	2.72 ns	− 1.76 ns	− 1.10 ns	− 0.14 ns	1.17 ns	0.02 ns	− 0.32 ns	0.79 ns	5.90 ns	− 2.81 ns	0.38 ns	− 1.41 ns
ARC68 × ARC9	− 1.23 ns	1.91 ns	− 1.23 ns	0.49 ns	0.55 ns	0.94 ns	− 0.22 ns	− 6.50 ns	− 3.71 ns	− 0.53 ns	− 1.69 ns	− 0.86 ns	− − 25.96**
ARC8 × ARC9	1.26 ns	− 2.05 ns	− 3.45*	1.57*	− 0.73 ns	− 1.03 ns	− 0.26 ns	14.69 ns	4.23 ns	− 3.96 ns	1.15 ns	1.55*	− 0.98 ns

indicated a favourable recombination of alleles donated by the individual parents. Thus, the newly developed crosses with high yield potential are recommended for genetic advancement employing the pedigree or pure line selection methods to advance the best selected F_2 individual plants to F_3 and advanced generations to select homozygous plants and homogeneous lines. The F_8 elite candidate lines will be tested for yield stability across representative growing environments. High-performing lines will be recommended and registered as new varieties in South Africa or similar agro-ecologies. Also, the yield of the newly-developed crosses is higher than that of the popular variety MPB 51 (Brianbeek), which is widely cultivated in South Africa (Mabhaudhi et al. 2014). Also, the yield attained for most crosses is comparable to the MPB39 landrace, which is popularly grown in KwaZulu-Natal (Musango et al. 2022). However, the new crosses have desirable shorter days to 75% maturity than this landrace.

Quantitative agronomic traits are governed by multiple genes, allowing differential genotype response to environment factors (Esan et al. 2023). The test locations rendered variable trait expressions of the assessed parents and crosses (Table 4). For example, the GCA and SCA effects had significant interactions with locations. The interaction effects suggest that the GCA effects of parents and the SCA effects of crosses were location-specific. Therefore, genetic advancement and selection of promising progenies should be undertaken across representative growing environments to guide the selection of the best lines with narrow or broad adaptation. The test locations reportedly contribute to the expression of agronomic traits in Bambara groundnut, including the number of secondary branches, pod length, number of pods per plant and grain yield (Jonah et al. 2010).

Genotype-by-environment interaction is the leading cause of the varied performance of genotypes when grown under different production environments. Several studies have reported significant genotype $\times$ environment interaction for Bambara groundnut agronomic performance and yield potential (Sari et al. 2021; Modi et al. 2022; Paulos et al. 2022). In the present study, genotype $\times$ location (environment) interaction effects were notable for studied agronomic traits (Table 2). These provide opportunities and challenges for selecting desirable genotypes. Genotypes that perform consistently higher across all the test

locations are considered widely adaptable. However, some genotypes perform exceptionally well in one location. These have specific adaptations to an environment. Parental lines, including ARC Bamb 55, ARC Bamb 109 and ARC Bamb 104, had an overall high mean performance, but ARC Bamb 55 was specifically adapted to Loskop while ARC Bamb 104 was superior at Brits site. Among the crosses, ARC9 $\times$ ARC44, ARC6 $\times$ ARC25 and ARC9 $\times$ ARC6 were the overall best genotypes for yield potential, but ARC9 $\times$ ARC44 was superior at Loskop, and ARC6 $\times$ ARC25 was the best at Brits. The crosses that exhibit specific adaptation should be used to develop cultivars for the target production environment. However, broad adaptation should be sought in breeding populations to allow the germplasm to wider production. Germplasm with limited areas of adaptation will limit germplasm exchange.

The GCA effects of the parental lines on several traits were significant, suggesting that the traits were conditioned by additive gene effects (Onwubiko et al. 2019). However, in the present study the variances for location $\times$ GCA interaction effects were significant, indicating the role of the environmental factors in additive gene expression. Traits with significant and positive GCA effects can be exploited by selecting parental lines with desirable characteristics to develop higher-performing progenies. Grain yield, stem branching and crop maturity are essential traits in developing Bambara groundnut varieties. Two parents, ARC Bamb 25 and ARC Bamb 66, were good general combiners for grain yield per plant and hundred seed weight (Table 4), which indicates that these parents are ideal for developing breeding populations. Parental lines with desirable GCA effects are the best candidates for varietal development in self-pollinating species.

Traits with significant SCA effects indicate that non-additive gene effects primarily cause trait inheritance. Non-additive gene effects arise from the interaction of alleles from diverse parents (Hochholdinger and Baldauf 2018). If the allelic interaction is favourable, the resultant progeny performs superior to the parents involved due to dominance, overdominance or epistasis. SCA effects represent the non-additive proportion of variance that is difficult to exploit in trait improvement in self-pollinating crops due to low heritability and unpredictability of reshuffling of genes. The specific combining ability effect relates to

the performance of some crosses, which is relatively better or worse than would be expected based on the average performance of the parents involved. Osei et al. (2014) reported that selecting crosses with superior performance compared to their parents enhanced genetic gain in breeding through favourable gene recombination.

For developing early maturing breeding populations, crosses with negative SCA effects for days to 75% maturity are desirable for selection. These crosses include ARC25 $\times$ ARC55, ARC25 $\times$ ARC55, ARC25 $\times$ ARC68, ARC25 $\times$ ARC8, ARC42 $\times$ ARC57, ARC42 $\times$ ARC6, ARC42 $\times$ ARC66, ARC42 $\times$ ARC68, ARC44 $\times$ ARC55, ARC44 $\times$ ARC57, ARC44 $\times$ ARC6 and ARC44 $\times$ ARC66 (Table 5). Early maturing varieties are ideal for marginal environments such as those mostly found in sub-Saharan Africa, characterised by inadequate rainfall and high temperatures. However, earliness to maturity can lead to yield penalties in environments where soil moisture and other growing conditions are favourable.

High SCA effects for yield and related traits are desirable as they transmit additive genes during selection (Dholariya et al. 2014). The best hybrids selected in this study were ARC25 $\times$ ARC8 for grain yield per plant and number of nodes per stem, ARC42 $\times$ ARC8 for NSB, ARC25 $\times$ ARC8 for early maturity, ARC42 $\times$ ARC55 for number of pods per plant and ARC42 $\times$ ARC57 for seed width. This indicates that the parents are good combiners; hence their crosses are selected for improving yield and related trait. These crosses can generate novel breeding populations from which best-performing individuals with favourable agronomic characteristics can be selected for variety development. However, since the dominance, over-dominance and epistatic components are random and cannot be predicted, it will be difficult to breed for traits that are predominantly controlled by SCA effects (Wade 2001; Kristensen and Sørensen 2005). Furthermore, the SCA variance for most traits exhibited significant interactions with environmental effects. This means that the expression of SCA effects varied over the test locations, which makes breeding efforts even more complicated when attempting to exploit this component of trait inheritance.

Understanding the genetic control of agronomic traits is vital to guide selection in crop breeding programs. The ratio of GCA to SCA variances provides

a valuable measure of trait control (Shaibu et al. 2018). GCA/SCA ratio > 1 indicates additive gene effects, while a ratio < 1 indicates of non-additive gene effects. In the present test populations, most traits exhibited GCA/SCA ratios < 1 , indicating that non-additive gene effects were preponderant, needing continuous selfing and selection of homozygous plants to accumulate additive gene action. The non-additive gene action found in this study were in concurrence with Shiferaw (2022), who reported that grain yield was controlled by non-additive gene action. Heritability is a useful measure of the proportion of variance observed among genotypes due to genetic differences and is expressed in a broad and narrow sense genetic control of traits (Oppong-Sekyere et al. 2019). Robinson et al. (1949) classified heritability values less than 30% as low, between 30 and 60% as moderate and above 60% as high. In the present study, heritability estimates for the number of nodes per stem, seed length, number of pods per plant and yield per pod were moderate, suggesting a high environmental influence on their expression. Similarly, Khaliqi et al. (2021) reported high heritability estimates for plant height, 100 seed weight, and harvest count in Bambara groundnut populations. High heritability estimates for seed yield were reported by (Rejeki et al. 2020). Conversely, the number of seeds per pod showed the lowest heritability (2.91%). This signifies that total phenotypic variance was primarily influenced by the environment, needing to delay the selection in advanced generations. The most suitable strategy for improving traits that are controlled by non-additive gene effects is through early generation selection of transgressive segregants. Advanced generation family selection is required for polygenes with additive genetic effect (Wang et al. 2018).

Conclusion

The present study assessed the combining ability effects and gene action of selected parents and newly developed crosses of Bambara groundnut for yield and related traits. The analysis allowed the identification of breeding parents and best-performing progenies for breeding and genetic advancement. The parental lines ARC Bamb25, ARC Bamb8 and ARC Bamb55 had positive and desirable GCA effects for grain yield per plant. The higher mean performance

of progenies compared to their parents suggests genetic gain in yield and related traits through breeding. The crosses ARC25 × ARC8, ARC44 × ARC9 and ARC6 × ARC9 had desirable SCA effects for grain yield per plant. Therefore, the newly developed families with high yield potential are recommended for selection and genetic advancement using pedigree or pure line selection methods for variety registration and commercialisation.

Acknowledgements Agricultural research Council acknowledged for funding and research material

Author contributions 1.3 Wrote main manuscript text 2.4 Reviewed manuscript 2. Funding

Funding Open access funding provided by University of KwaZulu-Natal. Agricultural Research Council Acknowledged for funding.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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