Beverage Plant Research

ARTICLE

Open Access

https://doi.org/10.48130/bpr-0025-0032

Beverage Plant Research **2026**, 6: e002

Estimates of combining ability for cocoa fat content in seeds of parental clones and their hybrids in diallel crosses

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Abstract

Cocoa butter or fat is one of the most valuable products extracted from cocoa beans. It is used for the manufacture of chocolate, pharmaceutical, and cosmetic products. Breeding programs in the world are trying to develop cocoa varieties with a high fat content and productivity to increase the production of fat per hectare. In a laborary, we extracted cocoa fat from seeds of 16 parental clonal genotypes and their 62 hybrid combinations tested in a field experiment. The hybrids plants were obtained by controlled pollination using a partial diallel mating design. Analysis of variance, Scott–Knott mean comparison tests, a test of the general combining ability (GCA) of parental clones, and tests of the specific combining ability (SCA) of hybrid combinations were performed. Significant differences were obtained for fat content in seed of the parental plants. Genotypes from the Amazon region demonstrated a higher fat content, whereas genotypes from Trinidad (Trinitario) and Criollo exhibited lower values. Diallel analysis indicated that both additive and nonadditive effects were relevant to fat content, with the additive effects having a greater influence. Regarding the fat content, it is recommended to use the parents SCA 6, CEPEC 89, BE 4, CCN 51, ICS 9, and P4B for crosses aiming to increase fat, whereas the genotypes EEG 29, CCN 10, and OC 67 should be avoided because of their tendency to reduce fat content.

Citation: Melo HL, Almeida AAFd, Pires JL, Silva GS, Barretto, et al. 2026. Estimates of combining ability for cocoa fat content in seeds of parental clones and their hybrids in diallel crosses. *Beverage Plant Research* 6: e002 https://doi.org/10.48130/bpr-0025-0032

Introduction

Cocoa (*Theobroma cacao* L.) is cultivated in the tropical regions of the American, African, Asian, and Oceanian continents to produce dried beans, which are roasted, shelled, and ground in mills to produce liquor, fat (butter), cake, and/or powder[1]. Cocoa butter is one of the most valuable products in the market and is of great industrial interest, particularly for the manufacture of chocolate, pharmaceutical, and cosmetic products[2]. It is predominantly composed of saturated fatty acids, palmitic and stearic acids, unsaturated fatty acids, oleic acids, and linoleic acids[3].

T. cacao has a great genetic variability for agronomic and industrial features that can be used by breeders to improve cultivars[4,5]. Generally, breeding programs in different cocoa-producing regions worldwide have focused on increasing productivity, pest resistance, larger pod and seed sizes, thinner pod shells, and self-compatibility[6,7]. However, programs that use recurrent selection, such as those in Côte d'Ivoire and Brazil (Comissão Executiva do Plano da Lavoura Cacaueira [CEPLAC]), are also trying to increase the fat percentage in seeds[8,9]. These programs produce hybrid and clonal cultivars, which are grown by farmers; however, selecting cultivars with higher fat content and better organoleptic quality has been facilitated by the increasing use of clonal cultivars[3,10].

The amount of butter in cocoa beans ranges from 45.4% to 60.3% (average = 53.2%), as shown by a study conducted in Brazil involving 490 cocoa accessions of different geographical origins[11]. Similar results were observed in 188 cocoa clones from Malaysia[12] and 35 accessions from the Brazilian Amazon[13]. This demonstrates a wide variation in fat content in cocoa accessions, allowing for the selection of superior genotypes.

The frequency distribution of fat content approximated a normal curve, suggesting that the inheritance of this trait is quantitative[11]. Fat content has low correlations with disease resistance, productivity, seed size, and pod size, making it an independent trait during selection work. Fat content exhibits a xenia effect, in which the origin of the pollen affects the expression of the the trait; therefore, selection can be made in the seed generation under analysis[14,15]. Regarding the genetic inheritance of fat content in cocoa, a study using an incomplete diallel design that evaluated 94 progenies in four locations in Malaysia demonstrated heritability ranging from 0.48% to 0.81% and significant additive genetic effects in all experiments, with dominant genetic effects being significant in only one[16]. In addition, a quantitative trait loci (QTL) of major effect, explaining 22% of the variation in fat content, was identified in a self-fertilized population of the clone TSH 516[17].

In general, studies of genetic inheritance of agronomc traits of interest in cacao are controlled by genes of additive effects with high general combining ability[18–21]. The aims of this study were to characterize the percentage of fat content found in the seeds of 16 parental clones and 62 hybrid combinations resulting from a partial diallel mating scheme, to obtain estimates of the general combining ability (GCA) of the parental clones, and to estimate the specific combining ability (SCA) of hybrid combinations resulting from partial diallel crossing among the 16 parents.

Materials and methods

Genetic material and experimentl design

In this study, cocoa seed fat was extracted from 16 parental clones and 62 progenies. The 16 parental clones were part of a reciprocal recurrent selection program at the Cocoa Research Center (Centro de Pesquisa do Cacau [CEPEC]), CEPLAC, Ilhéus-BA. These parents were selected according to several criteria, including geographical origin, genetic resistance to diseases such as witches' broom and black pod, pod and seed size, fat content, and molecular DNA patterns[22]. These 16 parental clones were grouped into two sets: Eight as mothers and eight as fathers (Table 1). They were crossed according to a partial diallel strategy, namely Design II of Comstock and Robinson[23], resulting in the production of 62 of 64 progenies. Two crosses were lost during this process.

In total, 16 clonal parents and their 62 progenies were evaluated in a randomized complete block design with two replicates of 20 plants per plot in an experiment at CEPEC. The plants were grown at a spacing of 3 m × 3 m, and data were collected during the productive phase of the plants, approximately 8 years after planting. The agronomic maintenance of the field trials followed the management scheme, fertilization, and disease control protocols adopted by CEPLAC[24].

Ten pods from different plants under the same treatment were collected from each plot, from which 10 seeds per pod (simple sampling) were collected, totaling a composite sample of 100 seeds per plot used for data collection. The pods originated from open pollination during the main crop season from September to November in 2011.

Fat percentage

The extraction of cocoa seed fat was based on a method described by the Association of Analytical Chemists[25], adopting the following procedure:

(1) We ground 100 cocoa seeds without testa from each genotype until a homogeneous fine mass was formed.

(2) The mass was dehydrated in an oven at 105 °C until a constant mass was obtained.

(3) For each genotype, a sample (5 g) was placed in a 250 mL beaker, 100 mL of 70 °C hydrochloric acid solution was added, and the beaker was placed on a hot plate for gentle boiling for 20 min.

(4) The digestion product was filtered through a medium-grade filter paper with a diameter of 15 cm, previously moistened and free of fat, using a glass funnel with a capacity of 150 mL.

(5) The filter paper with the moist sample was transferred to a Soxhlet cartridge and covered with degreased cotton. The cartridges were dried in an oven at 105 °C for 4 h.

(6) A 250 mL flask from the Soxhlet extractor set, previously dried and tared with glass beads to standardize boiling, was filled with 150 mL of petroleum ether or hexane (30–60 °C). The cartridge containing the sample was placed in the extractor and subjected to extraction for 4 h under continuous flow.

(7) Subsequently, the solvent was evaporated in a rotary evaporator, and the flask containing the fat was dried in an oven at 105 °C until complete evaporation of the solvent.

(8) The flask containing the dry matter was weighed, and the percentage of fat was calculated.

Statistical analysis

The analysis of variance (ANOVA) of the data was performed according to the statistical model:

$$Y_{ij} = \mu + g_i + b_j + e_{ij}$$

where, Y_{ij} is the value of the *ijk*-th observation relative to genotype *i* in the *j*-th block, μ is the effect of the overall mean, g_i is the effect of the *i*-th genotype, b_j is the effect of the *j*-th block, and e_{ij} is the effect of the experimental error associated with plot *ij*.

For comparisons between means, the Scott–Knott test was used at a 5% probability level.

Diallel analysis was performed according to the model proposed by Geraldi and Miranda[26]. This model is an adaptation of Griffing's Method IV[27], in which the effects of the GCA of each parent and the effects of the SCA of the hybrid combinations are estimated using data obtained from $p(p-1)/2$ F_1 hybrids[28].

The ANOVA of the diallel analysis was performed according to the following model:

$$Y_{ij} = m + 1/2(d_1 + d_2) + g_i + g'_j + s_{ij} + e_{ij}$$

where, Y_{ij} is the mean of the treatment involving the *i*-th parent from Group I (mother clones) and the *j*-th parent from Group II (father clones), *m* is the overall mean of the diallel, d_1 and d_2 are the contrasts involving the means of Groups I and II, g_i is the effect of the general combining ability of the *i*-th parent in Group I, g'_j is the effect of the

Table 1. Cocoa clones used as parents in Group I (mothers) and Group II (fathers), with their respective codes, geographical groups, and origins.

Clone		Code	Geographical group	Origin
Group I (mothers)	Belém 4	BE 4	Forastero: Lower Amazon	Belém-PA, Brazil
	Centro de Pesquisa do Cacau 89	CEPEC 89	Forastero	Itabuna-BA, Brazil
	Cruzeiro do Sul 07	CSUL 7	Forastero: Upper Amazon	Cruzeiro do Sul-AC, Brazil
	Estação Experimental de Goitacazes 29	EEG 29	Forastero: Lower Amazon	Espírito Santo, Brazil
	Imperial College Selections	ICS 98	Trinitario	Trinidad and Tobago
	Ocumare 67	OC 67	Criollo	Ocumare de la Costa-Aragua, Venezuela
	Rio Branco	RB 39	Forastero	Rio Branco-AC, Brazil
	Scavina 6	SCA 6	Forastero: Upper Amazon	Ucayali River, Peru
Group II (fathers)	Cacao Castro Naranjal 10	CCN 10	Forastero × Criollo (Hybrid)	Napo, Ecuador
	Cacao Castro Naranjal 51	CCN 51	Forastero × Criollo (Hybrid)	Napo, Ecuador
	Centro de Pesquisa do Cacau 86	CEPEC 86	Forastero	Itabuna-BA, Brazil
	Imperial College Selections	ICS 9	Trinitario	Trinidad and Tobago
	Iquitos Mixed Calabacillo 76	IMC 76	Forastero: Upper Amazon	Iquitos, Peru
	Nanay 33	NA 33	Forastero: Upper Amazon	Nanay River, Peru
	Pound 4/B	P4B	Forastero	–
	Selecciones Guatemaltecas 54	SGU 54	Forastero: Guianas	Los Brillantes, Guatemala

general combining ability of the *j*-th parent from Group II, s_{ij} is the effect of the specific combining ability of the *i*-th parent from Group I and the *j*-th parent from Group II, and e_{ij} is the experimental error.

Results and discussion

Characterization of seed fat percentage in parents and their hybrids

The ANOVA revealed significant differences in seed fat content among the treatments (Table 2). A significant difference between treatments was expected because the parents were heterozygous clones selected for their differences in seed fat content and other characteristics. The average fat content of the genotypes was 54.19%, which is close to the minimum fat content required by the industry (55%). These results are similar to those observed by Pires et al.[11], who analyzed 490 cacao genotypes from different geographic origins. Tucci et al.[29] identified fat content within a commercially interesting range only in the ICS 39, UF 677, and IAC 1 clones, attributing the observed differences to the genetic material used, although they also considered climatic conditions to be a factor influencing the fat content.

Regarding the breakdown of treatments, significant differences ($p < 0.01$) were observed for hybrids, clones, and hybrid versus clone interactions. The existence of significant differences between clones and hybrids indicates the possibility of identifying genotypes that differ from others in terms of seed fat content in both groups. The hybrid versus clone contrast indicated that they behaved differently under different treatments. This heterogeneity of the material allows the implementation of selection practices, which, in turn, can result in genetic gains by selecting superior genotypes.

The mean fat content percentages of cocoa seeds of the parental clones and hybrids are presented in Tables 3 and 4, respectively. The variation in fat content among clones ranged from 47.51% (OC 67) to 57.20% (CCN 51), and from 48.71% (EEG 29 × CCN 10) to 57.51% (CEPEC 89 × CEPEC 86). Significant differences between the means were detected using the Scott–Knott test at a 5% probability level. This indicated a variation of approximately 10% in fat content for both clones and hybrids, demonstrating a wide range for this trait within the evaluated population. The coefficient of variation (CV) was 1.25%, reflecting a high experimental precision.

In general, genotypes collected from the Amazon region (CSUL, SPA, NA, PA, CJ, POUND, and RB) tended to have fat contents within the commercially desirable range (> 54%), whereas genotypes from the Trinitario/Criollo collection (UF, SGU, OC, ICS, P, and CC) commonly exhibited lower values (< 53%). In addition, low fat content was observed in Ecuadorian genotypes (EET) and traditional cocoa populations from Bahia and Espírito Santo[11].

Table 2. Summary of the ANOVA for the percentage of fat content in cocoa seeds, based on data from hybrids and parent clones.

Source of variation	Degrees of freedom	Fat (mean square)
Blocks	1	4.79*
Genotypes	77	8.92*
Clones	15	15.73*
Hybrids	61	7.00*
Clones × hybrids	1	24.04*
Error	77	0.46
CV (%)		1.25
Overall mean		54.21

* Significant at 1% level by the *F*-test; CV: coefficient of variation.

The physical and chemical characteristics of cocoa seeds affect the final quality of beans processed to produce cocoa liquor and its derivatives. The clonal cultivar CCN 51 is highly productive, disease-resistant, and widely cultivated in Ecuador, Brazil, and Peru. Although it has a very acidic and watery pulp, resulting in beans with low organoleptic quality after traditional fermentation, its high fat content makes it a viable option for cocoa fat production.

Table 3. Mean values for fat content (%) in cocoa seed clones.

Clone		Fat (%)
Group I (mothers)	CEPEC 89	56.10 a
	CSUL 7	55.91 a
	ICS 98	53.94 b
	BE 4	53.87 b
	EEG 29	53.20 b
	SCA 6	52.86 b
	RB 39	52.01 b
	OC 67	47.51 d
Group II (fathers)	CCN 51	57.19 a
	P4B	55.84 a
	ICS 9	55.59 a
	CEPEC 86	55.44 a
	SGU 54	53.97 b
	CCN 10	53.03 b
	IMC 76	50.60 c
	NA 33	47.99 d

Means followed by the same letters belong to the same group according to the Scott–Knott test at 5% probability.

Table 4. Mean values for fat content (%) in seeds of hybrids originating from interclonal crosses of cocoa.

Hybrid	Fat (%)	Hybrid	Fat (%)
BE 4 × ICS 9	56.22 a	ICS 98 × IMC 76	57.18 a
BE 4 × CCN 10	55.93 a	ICS 98 × NA 33	55.96 a
BE 4 × NA 33	55.39 b	ICS 98 × CCN 51	55.93 a
BE 4 × P4B	55.17 b	ICS 98 × CCN 10	55.27 b
BE 4 × CCN 51	55.06 b	ICS 98 × ICS 9	54.04 b
BE 4 × IMC 76	54.97 b	ICS 98 × CEPEC 86	53.34 c
BE 4 × CEPEC 86	54.22 b	ICS 98 × P4B	52.44 c
BE 4 × SGU 54	51.48 d	ICS 98 × SGU 54	51.39 d
CEPEC 89 × CEPEC 86	57.50 a	OC 67 × CCN 51	56.49 a
CEPEC 89 × IMC 76	54.55 b	OC 67 × NA 33	54.87 b
CEPEC 89 × NA 33	54.37 b	OC 67 × IMC 76	54.82 b
CEPEC 89 × P4B	54.06 b	OC 67 × SGU 54	54.15 b
CEPEC 89 × CCN 51	53.46 c	OC 67 × ICS 9	54.13 b
CEPEC 89 × ICS 9	53.32 c	OC 67 × P4B	53.57 c
CEPEC 89 × SGU 54	53.10 c	OC 67 × CEPEC 86	49.98 e
CSUL 7 × CCN 51	56.77 a	RB 39 × CEPEC 86	57.29 a
CSUL 7 × NA 33	55.09 b	RB 39 × SGU 54	56.17 a
CSUL 7 × SGU 54	54.92 b	RB 39 × P4B	56.08 a
CSUL 7 × IMC 76	53.46 c	RB 39 × NA 33	55.87 a
CSUL 7 × ICS 9	52.57 c	RB 39 × CCN 51	55.16 b
CSUL 7 × CCN 10	52.30 c	RB 39 × ICS 9	54.18 b
CSUL 7 × P4B	51.97 c	RB 39 × CCN 10	53.69 c
CSUL 7 × CEPEC 86	51.83 c	RB 39 × IMC7 6	50.35 e
EEG 29 × CCN 51	56.72 a	SCA 6 × IMC 76	57.46 a
EEG 29 × NA 33	55.28 b	SCA 6 × ICS 9	56.61 a
EEG 29 × P4B	54.88 b	SCA 6 × CCN 51	56.34 a
EEG 29 × IMC 76	54.04 b	SCA 6 × P4B	56.03 a
EEG 29 × ICS 9	53.91 b	SCA 6 × CCN 10	55.48 b
EEG 29 × SGU 54	53.04 c	SCA 6 × NA 33	55.14 b
EEG 29 × CEPEC 86	52.65 c	SCA 6 × SGU 54	54.56 b
EEG 29 × CCN 10	48.70 f	SCA 6 × CEPEC 86	52.66 c

Means followed by the same letters belong to the same group according to the Scott–Knott test at 5% probability.

GCA and SCA for seed fat content percentage

In a cocoa breeding program, evaluating only the parental genotypes is insufficient, particularly for traits such as fat content, which have quantitative genetic inheritance. Therefore, it is essential to obtain information on the combined abilities of these genotypes[30]. According to the diallel analysis, significant differences ($p < 0.01$) were observed for GCA in Groups I and II, as well as for SCA in hybrid combinations for fat percentage (Table 5). This suggests that both additive and nonadditive genetic effects are important for the expression of this trait.

In other words, the values observed in the hybrids for each evaluated trait resulted from the parents' GCA and SCA. These findings align with those reported by Lockwood and Pang[16], who identified both additive and dominant genetic effects on fat content.

In the present study, the quadratic genetic components of the SCA and GCA for fat content were found to be similar. This proximity between GCA and SCA suggests that additive, dominant, and epistatic gene effects are involved in the expression of fat content in cocoa. Other studies have reported significant mean squares for GCA and SCA in production traits[19], with GCA effects being superior for traits related to pod size and seed weight[30,31], as well as pod production[32,33]. The same pattern was observed for the average seed weight per pod[34], and seed shape and size[35].

The parental clones that exhibited the highest GCA estimates were SCA 6, CEPEC 89, and BE 4 in Group I and CCN 51, ICS 9, and P4B in Group II (Table 6). Given the importance of increasing the fat content in cocoa breeding, these genotypes can be used for crosses in ongoing reciprocal recurrent selection programs to develop improved populations in Groups I and II with high frequencies of alleles or allele combinations that are favorable for increased fat content.

Clones EEG 29, CCN 10, and OC 67 presented the lowest estimates of GCA. These findings align with the results reported by Pires et al.[11], who reported a lower average fat content (< 53%) in the Trinitario/Criollo and Ecuadorian genotypes.

Among the hybrid combinations, ICS 98 × IMC 76, CEPEC 89 × CEPEC 86, and SCA 6 × IMC 76 had values of around three, whereas OC 67 × NA 33, RB 39 × SGU 54, OC 67 × IMC 76, OC 67 × CCN 51, EEG 29 × NA 33, BE 4 × CCN 10, ICS 98 × NA 33, RB 39 × NA 33, and OC 67 × SGU 54 had values of around two (Table 7). Hybrid individuals from these progenies, characterized by a high fat content, productivity, and disease resistance, can be selected and multiplied through vegetative propagation and subsequently utilized in competitive clone trials aimed at developing superior clonal cultivars.

In a reciprocal recurrent selection program, it is crucial to obtain parental genotypes with high and positive GCA estimates for the trait. In addition, these parents should exhibit high SCA when crossing Groups I and II to achieve superior hybrids. Several parental genotypes listed in Table 7 met this criterion, demonstrating the potential for good allele complementarity in their combinations.

Fat content can be increased by enhancing the seed yield per hectare, increasing the amount of fat in the seeds, or both

Table 5. Summary of the ANOVA for GCA and SCA of cocoa clone parents from Groups I and II for fat content (%) in cocoa seeds based on analysis of the mean data from diallel crosses.

Source of variation	Degrees of freedom	Fat (mean square)
Treatments	79	8.7871**
Groups	1	2.2578*
GCA Group I	7	9.9113**
GCA Group II	7	11.8887**
SCA I × II	64	8.4269**
Error	77	0.4608
Effect of the mean		54.1872
Effect of d_1		−0.2656
Effect of d_2		0.2656

** and *: Significant at the 1% and 5% levels, respectively, by the *F*-test.

Table 6. Estimates of GCA of parental clones from Groups I and II for fat content (%) of cocoa seeds, based on the mean diallel cross data.

Clone		Fat
Group I (mothers)	BE 4	0.4050*
	CEPEC 89	0.4188*
	CSUL 7	−0.0484
	EEG 29	−0.4751
	ICS 98	0.1750
	OC 67	−1.3240
	RB 39	0.1245
	SCA 6	0.7241*
Group 2 (fathers)	CCN 10	−0.7303
	CCN 51	1.4939*
	CEPEC 86	−0.1698
	ICS 9	0.3156*
	IMC 76	−0.3623
	NA 33	−0.3690
	P4B	0.2922*
	SGU 54	−0.4703

* Clones showing high GCA.

Table 7. Estimates of SCA for fat content of cocoa seeds in hybrid combinations formed by parental genotypes from Groups I and II, derived from the mean of diallel cross data.

Hybrid	Fat	Hybrid	Fat
BE 4 × CCN 10	2.0731*	ICS 98 × CCN 10	1.6431
BE 4 × CCN 51	−1.0261	ICS 98 × CCN 51	0.0789
BE 4 × CEPEC 86	−0.2023	ICS 98 × CEPEC 86	−0.8523
BE 4 × ICS 9	1.3173	ICS 98 × ICS 9	−0.6377
BE 4 × IMC 76	0.7402	ICS 98 × IMC 76	3.1802*
BE 4 × NA 33	1.1718	ICS 98 × NA 33	1.9668*
BE 4 × P4B	0.2856	ICS 98 × P4B	−2.2144
BE 4 × SGU 54	−2.6369	ICS 98 × SGU 54	−2.5019
CEPEC 89 × CCN 10	−0.0990	OC 67 × CCN 10	0.2750
CEPEC 89 × CCN 51	−2.6400	OC 67 × CCN 51	2.1329*
CEPEC 89 × CEPEC 86	3.0688*	OC 67 × CEPEC 86	−2.7133
CEPEC 89 × ICS 9	−1.6016	OC 67 × ICS 9	0.9563
CEPEC 89 × IMC 76	0.3113	OC 67 × IMC 76	2.3192*
CEPEC 89 × NA 33	0.1379	OC 67 × NA 33	2.3808*
CEPEC 89 × P4B	−0.8333	OC 67 × P4B	0.4196
CEPEC89 × SGU54	−1.0358	OC 67 × SGU 54	1.7571
CSUL 7 × CCN 10	−1.1035	RB 39 × CCN 10	0.1135
CSUL 7 × CCN 51	1.1423	RB 39 × CCN 51	−0.6457
CSUL 7 × CEPEC 86	−2.1339	RB 39 × CEPEC 86	3.1531
CSUL 7 × ICS 9	−1.8843	RB 39 × ICS 9	−0.4423
CSUL 7 × IMC 76	−0.3114	RB 39 × IMC 76	−3.5944
CSUL 7 × NA 33	1.3202	RB 39 × NA 33	1.9322*
CSUL7 × P4B	−2.4560	RB 39 × P4B	1.4760
CSUL7 × SGU54	1.2565	RB 39 × SGU 54	2.3285*
EEG 29 × CCN 10	−4.2769	SCA 6 × CCN 10	1.2990
EEG 29 × CCN 51	1.5139	SCA 6 × CCN 51	−0.0652
EEG 29 × CEPEC 86	−0.8923	SCA 6 × CEPEC 86	−2.0814
EEG 29 × ICS 9	−0.1177	SCA 6 × ICS 9	1.3882
EEG 29 × IMC 76	0.6952	SCA 6 × IMC 76	2.9161*
EEG 29 × NA 33	1.9368*	SCA 6 × NA 33	0.6027
EEG 29 × P4B	0.8756	SCA 6 × P4B	0.8315
EEG 29 × SGU 54	−0.2019	SCA 6 × SGU 54	0.1190

* Hybrids showing high SCA.

simultaneously. The latter approach must consider that seed yield and fat percentage are not correlated and, in principle, are independent traits[14]. Therefore, during the selection process, it is important to identify parents that possess a high frequency of favorable alleles for these traits, either within the same genotype or across different genotypes, to develop segregating populations for selection.

Moreover, given the significant role of SCA in both fat content and yield, the development of improved populations through reciprocal recurrent selection schemes that provide good allele complementarity should be explored to obtain superior cultivars.

Conclusions

The evaluated genotypes, comprising 16 parental clones and 62 progenies, exhibited significant differences in seed fat content. These differences benefit breeding programs because genetic gains can be achieved by selecting superior genotypes. Additive effects were superior to dominant effects on fat content in cacao. The parents SCA 6, CEPEC 89, BE 4, CCN 51, ICS 9, and P4B can be recommended for crosses when the breeding program's goal is to increase seed fat content. Conversely, EEG 29, CCN 10, and OC 67 should not be used, as they tend to reduce the values of the trait under analysis.

Author contributions

The authors confirm their contributions to the paper as follows: study conception and design: Almeida AAFd, Pires JL, Santos EA, and Ahnert D; data collection: Melo HL; analysis and interpretation of results: Melo HL, Almeida AAFd, Barretto WS, Santos EA, and Ahnert D; draft manuscript preparation: Melo HL, Almeida AAFd, Silva GS, Zhang D, and Ahnert D. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are included in this published article.

Acknowledgments

The first author thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, for granting a fellowship for Master's study. The second author gratefully acknowledges the CNPq for granting a fellowship of scientific productivity. We thank CEPLAC for conducting the field experiment and laboratory analyses, and Editage (www.editage.com) for English language editing.

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

Received 7 February 2025; Revised 23 July 2025; Accepted 3 September 2025; Published online 15 January 2026

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