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Variability and combinatorial ability in fruit characters of new *Theobroma cacao* hybrids in Ecuador

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ABSTRACT: In Ecuador there is a high genetic variability of *Theobroma cacao* L. However, its cultivation is mainly based on few materials, so it is necessary to develop and study new hybrids for its use in genetic improvement and commercial plantations. The phenotypic variability in the characteristics of the cobs was evaluated in 10 families of intraspecific cacao hybrids established in the experimental farm "Teodomira" in the province of Manabí, Ecuador, considering qualitative and quantitative descriptors. The specific combining ability (HCE) was calculated in the crosses made and the heritability of the quantitative characters. It was determined that there is a high genetic variability in the characteristics of the fruit at the inter- and intra-family level. However, most of the trees of the families analyzed have elliptical (44%) and ovoid (38%) cobs; more than 50% of the individuals presented cobs with obtuse apex, slight or absent basal constriction, medium or slight roughness, and intense yellow color pigmentation on the back; the average size of the cobs was 17.4 cm long and 8.1 cm diameter; fruit weight was between 624.3 and 422 g; seed weight per pod fluctuated between 130 and 96 g; and an average of 40 seeds per cob. The progeny obtained from the cross CCN51 × EET 103 presented the best HCE in terms of yield and seed weight. The evaluated characteristics of the cobs presented high and medium heritability (41-91%). There is a high genetic variability in the characteristics of the fruit of *T. cacao*, so it is possible to identify and select plants and progenies with desirable characteristics. Based on the calculated heritability, phenotypic selection is a suitable breeding method for this species.

Key words: crosses; cacao cobs; heritability; morphological descriptors

Variabilidad y habilidad combinatoria en caracteres del fruto en nuevos híbridos de *Theobroma cacao* en Ecuador

RESUMEN: En Ecuador existe una alta variabilidad genética de *Theobroma cacao* L. Sin embargo, su cultivo se basa principalmente en pocos materiales, por lo que es necesario el desarrollo y estudio de nuevos híbridos para su uso en mejoramiento genético y plantaciones comerciales. Se evaluó la variabilidad fenotípica en las características de las mazorcas en 10 familias de híbridos intraespecíficos de cacao establecidos en la finca experimental "Teodomira" en la provincia de Manabí, Ecuador, considerando descriptores cualitativos y cuantitativos. Se calculó la habilidad combinatoria específica (HCE) en los cruzamientos realizados y la heredabilidad de los caracteres cuantitativos. Se determinó que existe una alta variabilidad genética en las características del fruto a nivel inter e intrafamiliar. No obstante, la mayoría de los árboles de las familias analizadas tienen mazorcas elípticas (44%) y ovoides (38%); más del 50% de los individuos presentó mazorcas con ápice obtuso, constricción basal ligera o ausente, rugosidad intermedia o ligera, pigmentación intensa en el lomo, color amarillo. El tamaño promedio de las mazorcas fue 17,4 cm de largo y 8,1 cm de diámetro; peso de fruto varió entre 624,3 y 422 g; peso de semillas por mazorca fluctuó entre 130 y 96 g; un promedio de 40 semillas por mazorca. La progenie obtenida del cruzamiento CCN51 × EET 103 presentó la mejor HCE en cuanto a rendimiento y peso de las semillas. Las características evaluadas de las mazorcas presentaron heredabilidad alta y media (41-91%). Existe una alta variabilidad genética en las características del fruto de *T. cacao*, por lo que es posible identificar y seleccionar plantas y progenies con características deseables. Según la heredabilidad calculada, la selección fenotípica es un método de mejoramiento genético adecuado para esta especie.

Palabras clave: cruzamientos; mazorcas de cacao; heredabilidad; descriptores morfológicos

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Introduction

Theobroma cacao L. represents an important item in the global market, involving between 5 and 6 million farmers, generating between 2019 and 2020 more than 4.7 million tons of cacao. In this period, Latin America exported 18.4% (0.9 million tons), with Côte d'Ivoire and Ghana being the first two countries with the highest production (2.1 and 0.8 million tons respectively), followed by Ecuador (0.32 million tons) (Garcia et al., 2021). In Ecuador, the main crops grown are Nacional type cacao (materials native to the country) and the Trinitario clone CCN-51 (Motamayor et al., 2008; Jaimez et al., 2022). National cacao is recognized in international markets as a quality product for its organoleptic qualities; while CCN-51 is recognized for its productivity and disease tolerance (Sánchez-Mora et al., 2015). According to the Ministry of Agriculture and Livestock (MAGAP, 2021), there are 626,962 ha under cultivation in Ecuador, with a production of 330,872 tons and an average yield of 0.61 tons of seed per hectare (t ha^{-1}), with the main producing provinces being: Los Ríos (21.85%), Manabí (20.74%), Guayas (18.41%) and Esmeraldas (17.17%).

Ecuador, the country of origin and domestication of cacao (Zarrillo et al., 2018), has a wide genetic diversity, reflected in plantations over 70 years old that still remain on farmers farms. This diversity has been used for the genetic improvement of the species and has allowed the release of new varieties of Nacional type cacao (Quiroz-Vera et al., 2021). However, it is still necessary to continue developing new cultivars with good yields, disease resistance and excellent organoleptic quality that are adapted to the producing areas of the country. The formation of cacao hybrid families, using selected parents is one of the strategies used in the genetic improvement of cacao (Tarqui et al., 2017), to subsequently carry out selection and fix the genotype through asexual reproduction.

The generation of new cacao genotypes brings with it the need to study the agronomic behavior of plants, from their initial stage to their production in the field, as well as their interaction in different environments (Chávez et al., 2020). The importance of phenotypic characterization lies in being able to provide certification from the initial stage of the crop, generating knowledge about its morphological and/or productive characteristics and strictly specifying the variety with an approximation of its behavior under growing conditions. For this purpose, morphological descriptors are available for each genotype studied, which provide ordered information on their quantitative and qualitative characteristics of the different materials (Rangel et al., 2012). The qualitative and quantitative characteristics of a species have a wide range of variation, being important for the identification of promising individuals in breeding programs, and for the study of genetic parameters and phenotype-environment interaction. With this background, the objective of this study was to evaluate the genetic variability in cacao hybrid families based on their fruit characteristics, in order to identify candidate trees for use in the next phase of the breeding program.

Materials and Methods

Location of the study area

The study was conducted in the trial "Development of intraspecific hybrids of cacao for the province of Manabi", established in February 2018 at the Experimental Campus "Teodomira" of the Faculty of Agricultural Engineering, Technical University of Manabi, located in the Santa Ana canton of the province of Manabi, in the basin of the Portoviejo River at 60 masl. The study was conducted during the period January 2020 to January 2023 (fruit phenotypic data were taken in 2021 and pod production data during 2020-2023). Climatic conditions during the study period were: average temperature of 24.6 °C, relative humidity of 70 to 90%, annual rainfall of 500 mm. The site has a flat topography, according to USDA taxonomy the soil corresponds to the order vertisols with plastic clays, and according to the Köpen classification the climate is semi-arid warm (BSh).

Plant material

Ten families of intraspecific cacao hybrids were evaluated, 9 to 12 individuals per family, which were obtained through controlled crosses using commercial genotypes from the Pichilingue Tropical Experiment Station (Ecuador) and the CCN51 genotype as parents, selected for their high yield and disease tolerance (Table 1).

Table 1. Coding and origin of *Theobroma cacao* materials evaluated.

Codes/Description	Origin
F7-UTM - (NATIONAL × NATIONAL)	EET-544 × EET-103
F10-UTM - (NATIONAL × NATIONAL)	EET-103 × EET-554
F12-UTM - (NATIONAL × NATIONAL)	EET-554 × EET-558
F13-UTM - (NATIONAL × TRINITARY)	EET-103 × CCN-51
F14-UTM - (NATIONAL × TRINITARY)	EET-558 × CCN-51
F15-UTM - (NATIONAL × NATIONAL)	EET-103 × EET-558
F16-UTM - (TRINITARY × NATIONAL)	CCN-51 × EET-103
F18-UTM - (NATIONAL × NATIONAL)	EET-575 × EET-103
F19-UTM - (NATIONAL × TRINITARY)	EET-544 × CCN-51
F23-UTM - (NATIONAL × NATIONAL)	EET-95 × EET-558

Morphological characterization

Qualitative variables were determined by direct observation using a predetermined scale and morphological descriptors proposed by Engels et al. (1980). Quantitative variables were related to fruit size and weight, and seed weight and quantity (Table 2).

Data analysis

For each qualitative variable, the percentage of individuals within each family that presented the different categories was calculated. To facilitate the analysis, graphs were made with GraphPad Prism software, version 5.01. For quantitative

Table 2. Morphological descriptors for the characterization of *T. cacao* fruits.

	Variables	Indicator
Qualitative	Fruit shape	1=oblong, 2=elliptical, 3=ovoid, 4=spherical, 5=oblate (broad at the poles)
	Apex of cob	1=attenuated, 2=sharp, 3=obtuse, 4=rounded, 5=breast-shaped, 6=tooth-shaped
	Basal constriction shape	0=absent, 1=slightly present, 2=intermediate, 3=accentuated, 4=extensive, 4=extensive
	Surface roughness of the fruit	0=absent, 1=slightly rough, 2=intermediate, 3=intense roughness
	Anthocyanin intensity in unripe fruit backs	0=absent, 1=slight, 2=intermediate, 3=intense
	Anthocyanin intensity in primary grooves of unripe fruit	0=absent, 1=slight, 2=intermediate, 3=intense
	Color of ripe fruit	1=yellow, 2=red, 3=green
Quantitative	Fruit weight (g)	
	Fruit length (cm)	
	Fruit width (cm)	
	Shell weight (g)	
	Seed weight (g)	
	Number of seeds	
	Spine thickness (mm)	
	Cobs harvested	

variables, the normality of the data was previously analyzed using the Kolmogorov-Smirnov test and the homegeneity of variances using the Levene test. Data were arranged following a completely randomized design; mean, variance and standard deviation were calculated; in addition, analysis of variance (ANOVA) and comparison of means by Tukey test ($p < 0.05$) were performed using SAS 9.4 software (SAS Institute, Cary, NC, USA). The specific combining ability was analyzed, estimating the difference between the result of the crosses and the mean of the parents. Heritability (h^2) was calculated in a broad sense ($h^2 = (G_V/P_V) \times 100$) by estimating the phenotypic variance (P_V) of each variable as the deviation of the data from the overall mean, mean environmental variance (E_V) was calculated as the deviation from the mean of the individuals in each family, and genetic variance (G_V) as the difference between P_V and E_V.

Results and Discussion

Qualitative variables in cacao pods

The families of *T. cacao* evaluated show variability in the qualitative characters of fruits, both in shape, basal constriction and apex. It was recorded that most of the trees of the families analyzed have elliptical (44%) and ovoid (38%) cobs. At the intra-family level there is less variability in F19 with 70% of individuals with elliptical cobs. Only families F18 and F19 have spherical fruits (20%). Five variants of the fruit apex were recorded in the cacao trees evaluated. On average, 55% of the individuals presented ears with obtuse apex, being F12 the family that presented the highest percentage of individuals (80%) with this type of apex. Only 2 of the 10 families evaluated had ears with attenuated apices F15 (80%) and F16 (10%) (Figure 1).

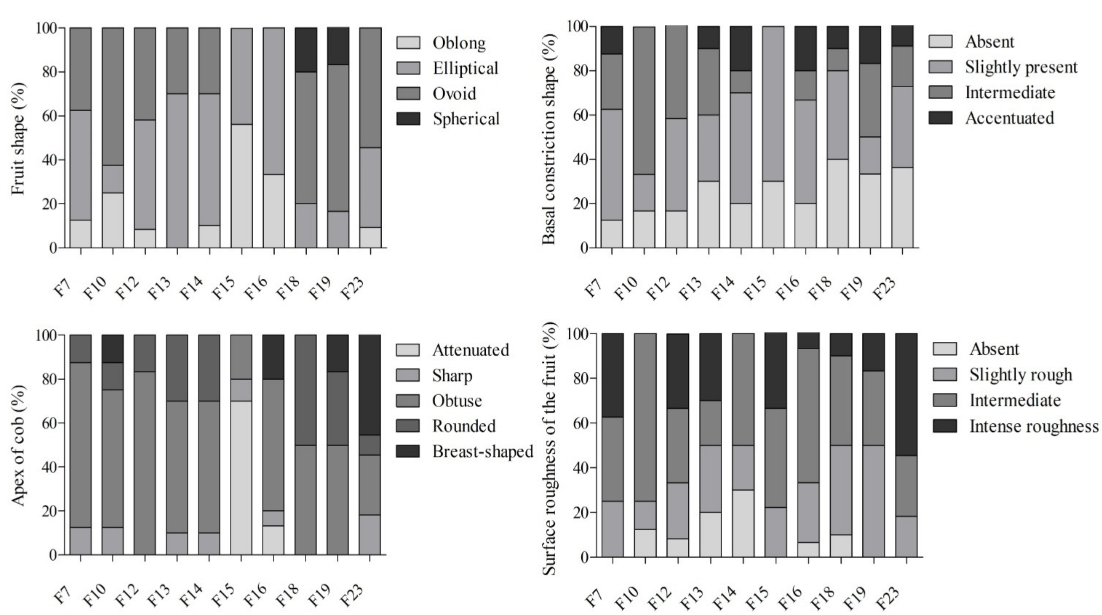

Figure 1. Fruit shape in 10 families of intraspecific hybrids of *T. cacao* established in the experimental campus "Teodomira", Manabí, Ecuador, 2021.

Likewise Ramírez et al. (2018) recorded variability in fruit shape in Criollo × Forastero cacao plantations in the lower Amazon, and in hybrid and Criollo cacao in germplasm banks, who conclude that the variability in this and other characteristics, reflect the hybridization that has occurred over time of Criollo × Forastero cacao from the lower Amazon. Five fruit apex variants were recorded in the cacao trees evaluated, similar to that reported by Maharaj et al. (2011), who also found a wide variation in this characteristic in selected hybrids from Trinidad.

According to their basal constriction, 7 of the 10 families evaluated had trees with four types of cobs. More than 50% of the trees in the families evaluated have cobs with slight or absent basal constriction. The family with the least variability in this characteristic was F15 with 70% of individuals with slight basal constriction and 20% with no basal constriction. As for surface roughness, 50% of the families have individuals with all four categories in this variable. However, most of the trees of the families evaluated have cobs with intermediate or light roughness, with the exception of F23, which has 60% of individuals with intense roughness (Figure 1).

Other authors have recorded a higher percentage of individuals with cobs with this type of basal constriction. Ramos et al. (2020) who evaluated criollo and ICS hybrids, Ramírez et al. (2018) in plantations of forastero cacao in Mexico, Vásquez et al. (2022) who evaluated cacao accessions in a germplasm bank in Peru; precisely the characteristic of absence of basal strangling are more frequent in Amazonian forastero materials. In terms of surface roughness, most of the trees of the families evaluated have cobs with intermediate or light roughness. Similarly, Maharaj et al. (2011) found that most of the selected hybrids from Trinidad (11 out of 12) had fruits with intermediate to intense roughness. On the other hand, Oliva et al. (2021), in native plantations of fine aroma cacao in northwestern Peru, recorded 68% in cacao pods with intermediate roughness.

Regarding the intensity of anthocyanin in the fruit backs and primary grooves of immature fruits, there is variability between and within the families analyzed; being more frequent the individuals with fruits with intense pigmentation in the back (52%), and intense pigmentation in the primary grooves (65%). Likewise, inter- and intra-family variability was recorded in the ripe fruit color trait. On average, 60% of the families evaluated had more than 50% of individuals with yellow coloration, 27% with red coloration and 13% with green coloration. Among the most homogeneous families for this characteristic is F14 with 90% of yellow fruit, and F15 with 90% of individuals with red fruit (Figure 2).

High pigmentation on immature fruit loin is not frequent in foraster cacao (Ramírez et al., 2018; Oliva et al., 2021) and is absent in 60% of selected Trinidad hybrids evaluated by Maharaj et al. (2011). Likewise, inter- and intra-family variability was recorded in the ripe fruit color trait. It should be noted that families F12, F15, F18 and F23, which have 10-90% of individuals with red fruits, are the result of crosses between National Type parents with yellow pods

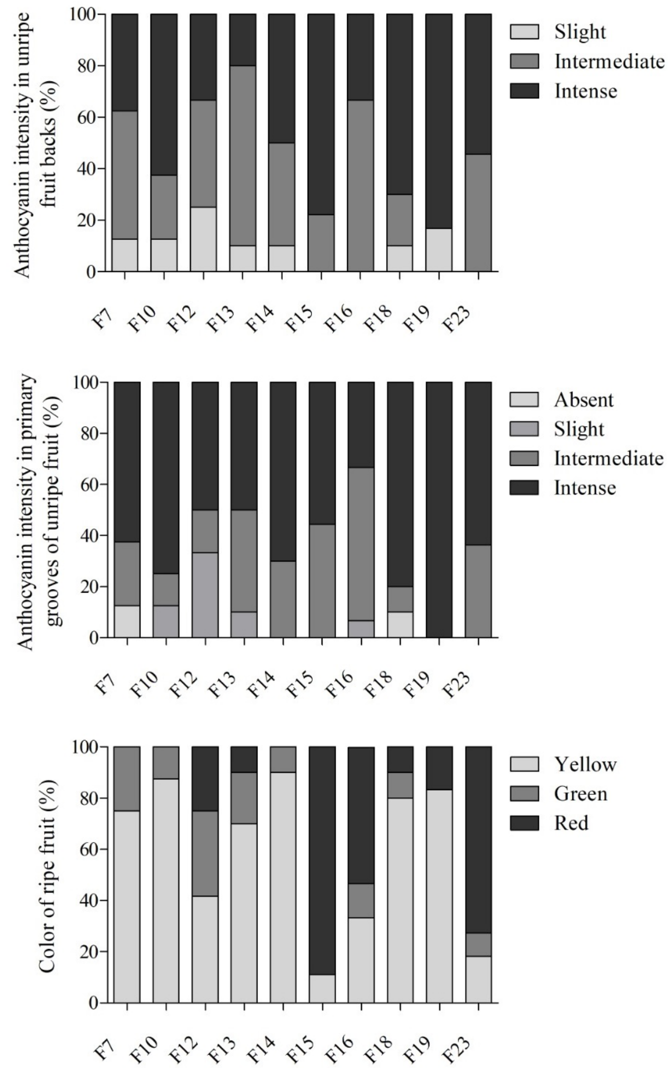

Figure 2. Fruit coloration in 10 families of intraspecific hybrids of *Theobroma cacao* established at the experimental campus "Teodomira", Manabí, Ecuador, 2021.

(a typical characteristic of foreign cacao from the lower Amazon), so their color would indicate genetic segregation. Likewise, Ramírez et al. (2018) found variability in fruit color in cacao materials, although most of them yellow (83% yellow in forastero cacao plantations, 83% yellow in hybrid germplasm, 36% yellow green in criollo cacao germplasm); and Ramos et al. (2020) who characterized cobs from 11 materials, of which 6 were yellow (4 criollo genotypes and 2 ICS genotypes (greenish yellow).

Quantitative variables in cacao pods

The trees evaluated showed variability within and among families in the characters of ear size and weight. Significant differences were detected among the families evaluated for the variables size ($p = 0.0001$) and cob weight ($p = 0.0025$), there is also variability within families (see standard deviation data) (Table 3). The average ear length was 17.4 ± 1.2 cm, ranging from 15.8 (F7) to 19.2 cm (F10). Fruit weight showed high variability, with the F10 family (624.34 g ± 30.72) having

Table 3. Quantitative variables of fruit and pod production in *T. cacao* progenies (10 individuals per family and 10 pods per individual) established in the experimental campus "Teodomira", Manabí, Ecuador. Values in parentheses represent the standard deviation (January 2020 to January 2023).

Family	FWe	FL	FD	SW	ShW	NS	LT	CH
F7	472.7 (132.9) b	15.8 (1.9) c	8.4 (0.71) ab	105.5 (30.27) ab	366.9 (110.65) b	40.6 (5.72) ab	16.1 (2.24)	20.9 (11.7) b
F10	624.3 (131.5) a	19.2 (1.5) a	8.8 (0.59) a	130.35 (29.29) a	493.9 (124.92) a	43.7 (5.31) a	17.1 (2.29)	18.2 (14.4) b
F12	423.3 (85.8) b	16.4 (1.7) bc	8.1b (0.55) c	102.5 (28.09) ab	320.8 (72.12) b	39.3 (7.70) ab	16.8 (1.83)	17.8 (11.4) c
F13	451.4 (119.5) b	16.7 (1.6) bc	8.1 (0.75) bc	95.1 (28.14) b	356.0 (101.77) b	36.9 (8.13) b	15.4 (2.18)	23.5 (15.3) b
F14	493.3 (144.5) b	17.8 (1.8) ab	8.1 (0.69) bc	114.4 (35.48) ab	377.2 (127.70) b	39.9 (8.20) ab	15.6 (2.05)	43.9 (20.0) a
F15	429.7 (97.1) b	18.6 (2.3) bc	7.8 (0.50) bc	105.1 (27.04) ab	324.5 (77.57) b	40.7 (8.68) ab	14.4 (2.12)	22.2 (14.8) b
F16	456.8 (115.0) b	18.1 (2.5) ab	7.8 (0.72) c	125.7 (33.12) a	332.0 (93.59) b	40.2 (8.49) ab	13.7 (1.76)	49.2 (13.9) a
F18	522.1 (141.6) ab	16.7 (2.1) bc	8.3 (0.87) abc	116.9 (30.28) ab	404.9 (130.96) ab	40.9 (7.98) ab	15.6 (2.41)	20.1 (12.9) b
F19	439.4 (112.9) b	17.8 (1.3) ab	7.9 (0.56) bc	103.5 (29.90) ab	335.9 (93.17) b	40.4 (6.52) ab	14.4 (1.86)	16.8 (11.7) c
F23	422.0 (96.7) b	16.4 (2.3) bc	7.8 (0.45) bc	107.4 (30.98) ab	314.6 (75.61) b	39.4 (8.33) ab	15.3 (2.17)	44.3 (14.6) a
Average	473.49	17.35	8.11	110.63	362.66	40.20	15.45	26.96
Variance	3837.68	1.22	0.10	121.48	2939.20	2.88	1.12	132.4
Probability	0.0001	<0.0001	<0.0001	0.0024	<0.0001	0.0610	0.1436	<0.0001

FWe - Fruit weight (g). FL - Fruit length (cm). FD - Fruit diameter (cm). SW - Seed weight (g). ShW - Shell weight (g). NS - Number of seeds. LT - Loin thickness (mm). CH - Average number of cobs/tree/year harvested January 2020- January 2023. Means with a common letter are not significantly different. Tukey (p ≤ 0.05).

the heaviest cobs and the F23 family having the lowest weight (421.99 g ± 26.20). Shell weight was statistically similar in 8 of the 10 families evaluated, with families F10 (493.9 g) and F18 (404.9 g) having the heaviest shell. Statistical differences were also recorded for the variable seed weight per ear (p = 0.0024), with families F16 (126 g/40.7) and F10 (130 g/43.7) having the heaviest seeds and F13 the lowest weight (96 g/36.8). The number of seeds was statistically similar in the families evaluated (40), with the exception of F13 which had a lower number of seeds (36.9) (Table 3).

Other researchers have also reported high variability in this trait, such as Ramírez et al. (2018), who in cacao plantations in Mexico recorded fruit weights ranging from 243.4 to 1194.3 g, and Maharaj et al. (2011) who found cacao cobs with weights ranging from 466 to 988 g in selected hybrids from Trinidad. Although fruit weight is a variable that is usually considered important in the evaluation and selection of elite trees, it is more important to consider the weight of the seeds, since sometimes the thick shell weighs more than the seeds.

The variable seed weight per ear was different among families; F16 and F10, which have the heaviest seeds, have a common parent, EET-103. It is important to mention that F16 had the best yield in harvested ears; on the contrary, F10 is one of the families with the lowest yield. Greater variability in seed weight per fruit reported by Ramírez et al. (2018) in plantations of forastero cacao of 27.3-178.3 g seeds/fruit, in hybrid cacao 69.9-196.0 g and in criollo cacao 52.9-140.7 g; and Farid et al. (2021) who determined an average of 72-135 g in superior cacao clones in Indonesia.

Of the 10 families evaluated, 9 had a similar number of seeds (40). Likewise, Ramos et al. (2020), when evaluating hybrid and criollo cacao, recorded a maximum number of 42 seeds per fruit. However, several researchers have determined a high variability in the number of seeds per fruit in different cacao genetic groups; among which, López et al. (2022) reported a selection of promising criollo cacao germplasm with greater variability around weight (0.17- 1.25 kg) and number of seeds per fruit (75- 21); Ramírez et al. (2018) in plantations of forastero cacao determined a range of 17.0 to 46.0 seeds/fruit, in hybrid cacao 21.0 to 51.8 and in criollo cacao between 29.8 and 38.8; Maharaj et al. (2011) recorded 42.2 to 61.4 seeds per fruit in selected hybrids from Trinidad; Farid et al. (2021) determined an average of 28 to 39 seeds per fruit in superior cacao clones in Indonesia.

These results demonstrate that the high variability in the material evaluated can be used in breeding programs for the selection of parents and/or hybrids with the desired characteristics. This high variability would be related to hybridization, being determinant for the identification and selection of elite plantations. It has been considered that heterosis and cross-fertilization can produce these variations in characters of interest for the selection of superior genotypes.

Combinatorial ability and heritability

There was a positive effect on ear weight in 50% of the families evaluated, especially in F10, corresponding to the cross EET-103 × EET-554 (hce = 61.3). However, in 5 families there was a negative effect, the highest in family F15, corresponding to the cross EET-103 × EET-558 (hce = -33.5). In cob size, fruit length had the highest positive effect for families F15 (hce = -0.3) and F16 (CCN-51 × EET-103) (hce = -0.2), and the highest negative effect on fruit diameter in the same families (1.1 and 0.7). Seed number (hce = 1.6) and seed weight (hce = 10.1) showed the highest positive effects on F10 progeny. In contrast, there were negative effects on shell weight and loin thickness in the progeny of the F15 and F16 families. In the variable ear production, families F15 (hce = 55.5) and F16 (hce = 72) had the best specific combining ability (Table 4).

There was a positive effect on combining ability in more than 50% of the families evaluated for the variables ear weight, seed number and seed weight. In this sense, Mustiga et al. (2018) have reported positive effects for yield in specific cacao crosses; who also performed a preliminary comparison of the performance of clonal parents vs.

Table 4. Effect of specific combining ability on the size and production of pods in *T. cacao* progenies (10 individuals per family and 10 pods per individual) established in the experimental campus "Teodomira", Manabí, Ecuador (January 2020 to January 2023).

	FWe	FL	FD	SW	ShW	NS	LT	CH
EET-544 × EET-103 (F7)	15.2	-1.2	0.3	-2.8	18.0	0.4	0.6	14.8
EET-103 × EET-554 (F10)	61.3	0.5	0.3	10.1	51.2	1.6	0.7	-29.7
EET-554 × EET-558 (F12)	-4.7	-0.6	0.1	-1.2	-3.4	-0.5	1.1	-0.6
EET-103 × CCN-51 (F13)	-27.5	-1.2	0.0	-12.0	-15.3	-3.0	0.1	10.1
EET-558 × CCN-51 (F14)	18.7	0.1	0.0	5.1	13.0	0.3	0.3	12.8
EET-103 × EET-558 (F15)	-33.5	1.1	-0.3	-2.2	-31.3	0.7	-1.3	55.5
CCN-51 × EET-103 (F16)	-13.4	0.7	-0.2	6.0	-18.8	-0.1	-0.9	72.0
EET-575 × EET-103 (F18)	19.3	-0.1	0.1	1.6	17.7	0.2	0.1	-48.5
EET-544 × CCN-51 (F19)	-4.2	0.5	-0.1	0.0	-3.9	0.8	-0.9	-17.0

FWe - Fruit weight (g). FL - Fruit length (cm). FD - Fruit diameter (cm). SW - Seed weight (g). ShW - Shell weight (g). NS - Number of seeds. LT - Loin thickness (mm). CH = Cobs harvested January 2020-January 2023.

progenies, suggesting the presence of heterobeltiosis in the family where there was the highest specific combining ability. So also, Padi et al. (2017) have reported positive effects on the specific combining ability of some crosses for yield and other variables, agreeing that there are strong non-additive genetic effects. Other researchers have analyzed both general combining ability and HCE, concluding that there are important additive and non-additive genetic effects, which should be considered for selecting parents and/or hybrids in cacao breeding programs (Pereira et al., 2017; Ofori et al., 2019; Ofori et al., 2020).

In husk weight, there were positive effects in the progenies of the F15 and F16 families, which have the best specific combining ability in the variable ear production (Table 4). This characteristic is important for the selection of promising individuals, since the thinner and lighter shelled cob would imply a greater investment of resources in the production of seeds and cobs.

Heritability in the broad sense for variables related to cacao pod size, weight and yield is moderate to high. It was calculated between 30 and 70% for length, between 40 and 80% for diameter and from 33 to 74% for ear weight. Seed weight and seed number were calculated in a range of 25 to 57% and 35 to 58%, respectively. The heritability of husk weight for the materials analyzed was calculated at 40% and for the thickness of the episperm on the cob loin was 83 to 95%. On average, ear production in the families evaluated has a heritability of 58% (Table 5).

Table 5. Variability and heritability in fruit traits in families of intraspecific hybrids of *T. cacao*, established at the experimental campus "Teodomira", Manabí, Ecuador (January 2020 to January 2023).

Family	Fruit weight			Fruit length			Fruit diameter			Seed weight		
	EV	GV	H	EV	GV	H	EV	GV	H	EV	GV	H
F7	4658.1	11527.2	71.2	1.7	3.6	67.2	0.4	0.1	42.4	610.0	437.0	41.7
F10	6852.5	9332.8	57.7	1.5	3.5	71.1	0.4	0.1	82.9	516.1	530.9	50.7
F12	4283.9	11901.4	73.5	1.5	3.6	69.0	0.2	0.3	60.9	520.3	526.6	50.3
F13	6852.5	9332.8	57.7	1.4	2.1	71.3	0.5	0.0	73.7	651.8	395.2	37.7
F14	11390.1	4795.2	32.7	2.9	2.7	52.9	0.3	0.2	50.6	448.1	598.9	57.2
F15	4742.8	11442.5	70.7	2.3	1.3	53.9	0.1	0.4	72.7	493.0	554.0	52.9
F16	7907.8	8277.5	57.3	3.8	2.3	26.8	0.3	0.2	46.2	593.8	453.2	43.3
F18	7246.8	8938.5	56.5	2.7	3.7	53.7	0.5	0.0	81.6	752.1	294.8	28.2
F19	9193.2	6992.1	72.2	1.4	1.5	73.2	0.3	0.2	49.7	784.9	262.1	25.0
F23	7006.2	9179.2	64.5	3.5	2.7	30.8	0.1	0.4	75.2	783.1	263.9	25.2
Average	7013.4	9171.9	61.4	2.3	2.7	57.0	0.3	0.2	63.6	615.3	431.6	41.2

	Number of sedes			Loin thickness			Cob harvested		
	EV	GV	H	EV	GV	H	EV	GV	H
F7	30.1	33.2	52.4	0.04	0.43	91.5	181.6	156.0	46.2
F10	26.4	36.8	58.2	0.05	0.42	89.8	128.9	208.6	61.8
F12	48.7	22.3	31.4	-	-	-	207.9	129.7	38.4
F13	52.7	28.4	35.0	0.05	0.42	89.3	104.4	233.2	69.1
F14	51.2	31.3	38.0	0.05	0.42	88.6	110.1	227.4	67.4
F15	56.6	66.0	53.8	0.03	0.44	94.6	117.8	219.7	65.1
F16	69.0	45.5	39.7	0.03	0.42	93.8	67.0	270.5	80.1
F18	63.2	30.1	32.2	0.08	0.39	83.0	172.4	165.2	48.9
F19	35.1	28.2	44.6	0.03	0.44	93.2	200.2	137.4	40.7
F23	59.0	18.7	24.1	-	-	-	123.3	214.3	62.0
Average	49.2	34.0	40.9	0.04	0.42	90.5	141.4	196.2	58.0

EV - Environmental variance; GV - Genetic variance; H - Heritability.

Coinciding with Doaré et al. (2020) who reported for fruit size a heritability of 54%; Cilas et al. (2010) 51% for seed weight and Doaré et al. (2020) 29% for seed number. Cilas et al. (2010) further corroborated that the variable seed number, which depends on pollination, is independent of ovule number, although ovule number has high heritability. DuVal et al. (2017) also calculated similar heritability in yield (37 to 64%) in a breeding program in Brazil. On their side Padi et al. (2017), Mustiga et al. (2018), and Ofori et al. (2019) calculated the heritability for the yield variable as 50, 56.7 and 49%, respectively, so they consider that there are significant non-additive effects in this characteristic.

Similar to that recorded in this study, Doaré et al. (2020) calculated 49% for the heritability of husk weight in clones of different genetic types established in the germplasm bank of CIRAD, France. However, a higher heritability was calculated for the thickness of the episperm on the cob loin (83 to 95%), a characteristic that the authors consider important for the selection of high-yielding trees for crop establishment, or parents in breeding programs. The calculated heritability indices show that morphological characteristics and cacao pod production depend on genotypes, but can also be influenced by the environment and crop management, including nutritional factors.

Conclusions

There is a high genetic variability in the fruit characteristics of *T. cacao*, inter and intra-family for the parameters evaluated, so it is possible to identify and select plants and progenies with high productivity and seed weight. Segregation was recorded in the characteristics of color, shape, roughness, apex, and basal constriction of the cobs.

The progeny obtained from the CCN51 × EET 103 cross showed the best specific combining ability in terms of yield and seed weight, showing favorable non-additive effects.

The evaluated characteristics of the pods showed high and medium heritability, which demonstrates that for the selection of cacao plants with the desired yield it is not necessary to use complex genetic improvement methods; a good morphoagronomic characterization and directed crosses would be sufficient.

Compliance with Ethical Standards

Author contributions: Conceptualization: LGC; Data curation: BGT; Formal analysis: FSM; Investigation: LGC, BGT; Methodology: LGC, BGT, FSM; Project administration: LGC; Writing – review & editing: LGC.

Conflict of interest: The authors declare that there is no conflict of interest (professional or financial) that might affect the manuscript. All the authors declare that they have read the manuscript.

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