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Combining-ability for cacao (*Theobroma cacao* L.) yield components under southern Bahia conditions

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Abstract The objective of this study was to assess five cacao cultivars (selfs) and 20 hybrids with regard to their general- and specific-combining ability for yield components using method 1, model I, of the diallel analysis system. The selfings and the hybrids were obtained through controlled crossings, tested in the field in a random block design with four replications and plots containing 16 plants. The experiment was set up in the Centro de Pesquisas do Cacau, in Itabuna, Bahia, Brasil, in 1975. The characteristics studied were: the number of healthy and collected fruits per plant (NHFP and NCFP), the weight of humid seeds per plant and per fruit (WHSP and WHSF), and the percentage of diseased fruits per plant (PDFP), for 5 years (1986–1990). The F-test values, highly significant for general combining ability (GCA) and specific combining ability (SCA), demonstrated the existence of variability for both effects. However, the effects of SCA were greater than those of GCA, when compared in terms of the average squared effects. This condition held for the characteristics NHFP, NCFP and WHSP, which shows the relative importance of the non-additive genetic effects over the additive effects. The reciprocal effects did not show significance. Breeding methods which explore the additive portion of genetic variance should be employed for obtaining higher-yielding cacao and high seed weight. For this, the segregant populations should involve cultivars CEPEC 1, SIAL 169 and ICS 1. Combinations involving the cultivar ICS 1 presented the most favorable results for the characteristics WHSP and WHSF, where the hybrid SIAL 169 × ICS 1 and its reciprocal were outstanding.

Key words *Theobroma cacao* L. · Combining ability Yield components · Genetic improvement

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Introduction

The development of superior hybrids has made a significant contribution to Brazilian cacao productivity. Hybrid cacao trees have permitted the renewal of crops with high and early yielding materials that also show some resistance to diseases. The hybrid type selected for commercial-scale production was similar to the intervarietal corn hybrid; a non-conventional hybrid synthesized from non-inbred clonal progenitors.

The progenitor clones, however, differ as to their combining ability for yield and, frequently, the yield ability of the clones per se is not associated with their performance as progenitors. Difficulties such as these were overcome by introducing combining-ability tests. With these tests a part of the randomness of the hybridization process was eliminated and the demand for area and for the time needed to assess the hybrid cacao trees was reduced.

In combining-ability studies the design most commonly utilized is the diallel design. In diallel analyses, Sprague and Tatum (1942) introduced the concepts of general combining ability (GCA) and specific combining ability (SCA). The GCA is a measure of the additive genic action, while the SCA is assumed to be a deviation from additivity. The combining ability in cacao for the characteristics of yield and resistance to diseases has been studied by a number of authors (Soria et al. 1974; Ojo 1982; Baez 1984; Engels 1985; Monteiro et al. 1985; Mora 1987; Pardo and Enriquez 1988; Tan 1990). The present study was undertaken for the purpose of estimating the general- and specific-combining ability of five cacao cultivars (selfs) and their 20 hybrids, at advanced ages.

Materials and methods

Five parent cacao cultivars of different origins, and their 20 hybrids obtained by diallel crossings, were assessed in the experimental area of the Centro de Pesquisas do Cacau (CEPEC), in Itabuna, Bahia. These cultivars, racial groups and their origins are described below:
(1) CC 41–Trinitario, originated from Costa Rica, Centro de Cacao;
(2) SIAL 169–Amazon, originated from southern Bahia, where it was selected by the now extinct Instituto Agronômico do Leste;
(3) CEPEC 1–Amazon, from southern Bahia, corresponding to the clone Catongo cultivar, selected as a spontaneous mutant with white seeds. It was named by the Centro de Pesquisas do Cacau;
(4) ICS 1–Trinitario, selected in Trinidad by the Imperial College of Tropical Agriculture;
(5) SIC 19–Amazon, selected in a single municipality of southern Bahia by the former Instituto de Cacau da Bahia.

The design employed was that of randomized blocks with 25 treatments (ten F_1s × ten reciprocals F_1s and five parents), with four replications and plots containing 16 plants spaced 3 m from each other. Temporary shading was produced by planting bananas at a similar spacing from the cacao trees. Definitive shading was provided by *Erythrina sp.* × every 24 m. The seeds for the crossings were obtained by controlled manual pollination in clonal cultivars. In turn, the cultivar seeds were obtained by selfing of the corresponding clones. The parent cultivars, all of them self-compatible, and the 20 possible hybrids were produced at CEPEC's germplasm bank in 1975. No mineral fertilization was used, only pest control. For the analysis of this study, data relating to monthly harvests effected from 1986 to 1990 were utilized, by considering the accumulated production of the agricultural year.

The data collected per plot were: the number of healthy and diseased fruit, the weight of humid seeds, the real number of plants (stands), and the number of productive plants. However, in assessing the parents and their crossings, the following items were considered: the number of healthy and collected fruits per plant (NHFP and NCFP), the weight of humid seeds per plant (WHSP) and per fruit (WHSF), and the percentage of diseased fruits per plant (PDFP). NHFP and NCFP represent the real and the potential production, respectively. WHSP, in kg, is the ratio between the weight of humid seeds per plot and the stand. WHSF, in g, is the ratio between the weight of humid seeds and the number of healthy fruits. PDFP represents the ratio between the number of diseased fruits and number of collected fruits. The latter characteristic was transformed by employing the square root of $x + 0.5$.

The individual analyses of variance were conducted annually for each characteristic, at the level of plot averages, according to the randomized block model. The genotypes studied were considered to be a selected sample of populations, characterizing fixed genotypical effects. The joint analysis of variance was conducted for each characteristic from aggregates of all the years, considering each year as a different environment. The analysis of combining ability was conducted from the results of the individual analysis to variance. In this case, the genotypes sums of squares were partitioned into general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (RE) by method 1, model I, of Griffing (1956). In assessing the GCA effects associated with each parent (g_i), the SCA effects associated with each crossing (s_{ij}), as well as the variance of the effects and the differences between effects, the same model was employed. The detection of the possible interactions of combining-ability effects with years was based on a joint analysis by the method discussed by Vencovsky and Barriga (1992).

Results and discussion

The overall mean of yield components for the five cultivars and their 20 hybrids are given in Table 1.

Table 1 Estimates of the means of the hybrids and cultivars for five characteristics over the combined years (1986–1990)

Genotype	(*ij*)	Means				
		NHFP	NCFP	WHSP	WHSF	PDFP
CC 41 × SIAL 169	12	48.840	52.946	4.475	91.238	2.614
SIAL 169 × CC 41	21	41.950	44.236	4.054	97.137	1.896
CC 41 × CEPEC 1	13	40.242	42.030	3.658	91.680	1.871
CEPEC 1 × CC 41	31	37.611	38.701	3.457	92.907	1.577
CC 41 × ICS 1	14	42.804	44.235	4.745	112.444	1.760
ICS 1 × CC 41	41	42.368	43.585	4.790	114.133	1.650
CC 41 × SIC 19	15	56.399	59.500	5.131	91.648	2.199
SIC 19 × CC 41	51	43.353	45.951	4.112	97.197	2.351
SIAL 169 × CEPEC 1	23	40.739	42.108	4.433	109.665	1.681
CEPEC 1 × SIAL 169	32	32.327	33.479	3.410	106.065	1.727
SIAL 169 × ICS 1	24	43.690	45.363	5.617	129.360	1.780
ICS 1 × SIAL 169	42	36.815	38.176	4.766	129.996	1.915
SIAL 169 × SIC 19	25	42.315	44.738	4.164	99.275	2.215
SIC 19 × SIAL 169	52	30.721	32.672	2.929	95.271	2.068
CEPEC 1 × ICS 1	34	34.157	34.741	4.249	125.070	1.382
ICS 1 × CEPEC 1	43	38.585	39.595	4.848	125.767	1.594
CEPEC 1 × SIC 19	35	36.925	38.084	3.703	100.270	1.575
SIC 19 × CEPEC 1	53	22.166	22.818	2.144	97.203	1.535
ICS 1 × SIC 19	45	41.170	42.795	4.931	120.579	1.806
SIC 19 × ICS 1	54	41.012	42.273	5.005	122.408	1.645
CC 41	11	32.254	33.620	2.620	80.930	1.898
SIAL 169	22	37.866	41.615	3.759	99.623	2.975
CEPEC 1	33	17.491	18.403	1.668	98.010	2.067
ICS 1	44	18.797	19.422	2.322	124.486	1.797
SIC 19	55	35.803	37.030	3.247	90.997	1.682
Means						
Hybrids		39.709	41.401	4.231	107.465	1.842
Cultivars		28.442	30.018	2.723	98.809	2.084
Overall		37.456	39.125	3.929	105.734	1.890

Means of yield components were 28.4, 30.0, 2.7 kg.pl^{-1}, 98.8 g.fruit^{-1} and 2.1% for the cultivars and 39.7, 41.4, 4.2 kg.pl^{-1}, 107.4 g.fruit^{-1} and 1.8% for the hybrids, with reference to NHFP, NCFP, WHSP, WHSF, and PDFP, respectively. This resulted in an average heterosis of 39.6, 37.9, 55.4, 8.8 and −11.6%, respectively. The hybrids outyielded the cultivars in all characters. However, the average heterosis obtained for fruit production, for example, was approximately half that reported by Atanda (1973) and Atanda and Toxopeus (1971).

The analysis of differences between genotypes, at the 1% level of significance, revealed the existence of variability for all of the characteristics. Such differences result, mainly, from the differences between the cultivars per se, of the hybrids, and of cultivars vs hybrids (Table 2). This situation reflects a condition very favorable for breeding. The heterogeneity of the material makes possible the implementation of selective practices and this, in turn, results in genetic gains by electing superior genotypes.

In view of the homogeneity of the error variances of the individual analyses, a joint analysis of variance was carried out, considering years as environments. The results of this analysis showed highly significant differences between the means of genotypes (G) and years (Y). However, no differential reaction of the genotypes in the 5 years of assessment was evident; that is, the G × Y interaction was not significant (Table 3). This absence of G × Y interaction, indicating that the genotypes did not alter the relative classification and performance over years, creates a very favorable condition both in terms of recommending cultivars to cacao planters as well as for the work of breeders. Considering years as representative, the breeder may practice selection based on only one or a few individual years. The explanation for the absence of interaction may be in the mixing of genotypes conferring greater stability in the presence of environmental variation. Another explanation may relate to the origin of the parents. Thus, three of the five parents

Table 2 Summary of individual analysis of variances in randomized blocks relating to five characteristics assessed in 25 cacao genotypes (1986–1990)

Year	Source	df	MS NHFP[a]	NCFP[b]	WHSP[c]	WHSF[d]	PDFP[e]
1986	Genotypes	24	496.595**	545.223**	6.829**	830.349**	1.048**
	Hybrids (H)	19	314.439**	360.729**	4.321**	745.082**	0.877**
	Cultivars (C)	4	454.022*	587.915**	3.999*	1 143.535**	1.081*
	H vs C	1	4 127.848**	3 879.824**	65.779**	1 197.672**	4.168**
	Error	72	129.856	133.048	1.307	37.943	0.368
Mean			50.076	52.143	5.163	103.265	1.989
CV%			22.756	22.121	22.141	5.965	30.513
1987	Genotypes	24	381.144**	395.089**	4.448**	983.695**	0.239
	Hybrids (H)	19	294.530**	303.113**	3.351**	906.704**	0.168
	Cultivars (C)	4	506.504**	601.683**	3.800**	1 180.770**	0.642*
	H vs C	1	1 309.373**	1 316.270**	27.876**	1 658.234**	0.003
	Error	72	85.409	85.924	0.769	56.778	0.187
Mean			40.403	40.836	4.078	101.622	1.152
CV%			22.874	22.699	21.504	7.415	37.495
1988	Genotypes	24	345.420**	382.131**	5.012**	676.437**	0.999**
	Hybrids (H)	19	212.754**	240.469**	3.160**	598.296**	0.853**
	Cultivars (C)	4	453.527*	628.560**	4.834**	830.504**	1.898**
	H vs C	1	2 073.649**	2 088.002**	40.909**	1 544.859**	0.176
	Error	72	92.036	94.788	1.056	42.750	0.233
Mean			36.517	37.296	4.022	110.338	1.410
CV%			26.271	26.105	25.548	5.926	33.523
1989	Genotypes	24	231.696**	247.260**	3.265**	933.766**	0.313
	Hybrids (H)	19	169.254**	187.495**	2.594**	866.342**	0.307
	Cultivars (C)	4	324.319**	324.082**	2.149*	1 160.988**	0.308
	H vs C	1	1 047.616**	1 075.509**	20.464**	1 305.922**	0.444
	Error	72	69.148	67.862	0.717	57.852	0.396
Mean			30.893	31.449	3.221	104.554	1.389
CV%			26.917	26.194	26.289	7.275	45.311
1990	Genotypes	24	266.062**	352.457**	3.617**	908.135**	2.339**
	Hybrids (H)	19	166.056*	242.143**	2.449**	852.345**	1.864*
	Cultivars (C)	4	255.202*	324.245*	1.517	1 275.336**	4.406**
	H vs C	1	2 209.607**	2 561.286**	34.204**	499.344**	3.111
	Error	72	89.745	98.958	0.895	62.391	0.899
Mean			29.391	33.900	3.164	108.888	3.510
CV%			32.232	29.344	29.909	7.254	27.013

*, ** Significant at the 5% and 1% level of probability, respectively
[a] Number of healthy fruits per plant–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

Table 3 Summary of the joint analysis of variance relating to five characteristics assessed in 25 cacao genotypes (1986–1990)

Source	*df*	MS				
		NHFP[a]	NCFP[b]	WHSP[c]	WHSF[d]	PDFP[e]
Blocks/years	15	253.429	308.121	3.489	124.633	2.863
Genotypes (G)	24	1498.839**	1712.938**	20.728**	4170.042**	2.603**
Hybrids (H)	19	968.767**	1150.930**	13.837**	3855.763**	1.913**
Cultivar (C)	4	1852.356**	2219.023**	13.164**	5206.591**	5.366**
H vs C	1	10156.133**	10366.730**	181.899**	5995.137**	4.673**
Years (Y)	4	6923.938**	6548.750**	65.986**	1387.750**	91.504**
G × Y	96	55.519	52.306	0.610	40.588	0.584
H × Y	76	47.067	45.755	0.509	28.254	0.539
C × Y	16	71.304	61.866	0.784	96.133	0.742
(H vs C) × Y	4	152.988	138.544	1.834	52.766	0.807
Pooled error	360	93.239	96.116	0.949	51.534	0.415
Mean		37.456	39.125	3.929	105.733	1.890
CV%		25.780	25.058	24.788	6.789	34.071

*,** Significant at the 5% and 1% level of probability, respectively
[a] Number of healthy fruits per plants–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

utilized in this study constitute the Bahia selections which, according to Mariano and Bartley (1981), exhibit relative uniformity and similar behavior, due to a high degree of parentage. On the other hand, the other two parents represent introduced material. Another factor that may exert an influence is the stabilization of the competition between cacao trees at an advanced age. This factor has received little attention in cacao studies.

The split of the sums of squares of genotypes into GCA, SCA and RE, for each characteristic and year, is shown in Table 4. The values of the mean squares of GCA were significant at the 1% level for all of the characteristics except for the percentage of diseased fruit (PDFP) in 1987, when it showed significance at 5%, and in 1989 when it was non-significant. In turn, with the exception off the character PDFP in the years 1987, 1989 and 1990, the values of the mean squares of SCA showed significance at 1%. For the five characteristics assessed, with the exception of the weight of humid seeds per plant (WHSP) in 1986, 1988 and 1990, the mean squares of GCA were always higher than those of SCA (Table 4). This indicates a possible predominance of additive genic effects over the non-additive. However, the high significance for GCA as well as SCA demonstrates the existence of variability due to both effects.

The superiority of the effects of GCA, in terms of mean squares, has been detected by Engels (1987) and Mora (1987) for characteristics relating to fruit size and seed weight, as well as for fruit production by Ojo (1982) and Tan (1990). The same situation occurred in Monteiro et al. (1985) in respect of the production of humid seeds per plant and the average weight of seed per fruit. There are also records of the superiority of GCA effects in cacao for the shape and size of seeds (Baez 1984). For the maximum number of seeds, the weight per fruit, and the production efficiency, the GCA was shown to be important by Engels (1985).

Actually, the comparison of the magnitudes of mean squares does not fully reflect the relative importance of the general- and specific-combining ability with reference to their genotypic components, as their respective mathematical expectations of the mean squares deduced by Griffing (1956) demonstrate. On the contrary, as asserted by Baker (1978), this procedure may lead to errors. On the other hand, the estimates of the average squared effects (components) reflect parameters which approximate to the variances of GCA and SCA obtained in the randomized model (model II). Thus, the estimates of average squared effects permit inferences about the relative importance of both the GCA and the SCA. The relative importance of average squared effects showed that, for the number of healthy and collected fruits (NHFP and NCFP) and the weight of humid seeds per plant (WHSP), the effects of SCA were much greater than those of GCA (Table 4) for the 5 years of this study. This indicates the importance of non-additive genetic effects in determining these yield components. For weight of seed per fruit (WHSF) and percentage of diseased fruit (PDFP), the additive genetic effects were more important. Therefore, for these two characteristics, breeding methods which explore the additive portion of the genotypical variance may be utilized for obtaining genetic gains.

With regard to reciprocal effects (RE) (Table 4), no significance was evident for most of the characteristics during the various years of this study. The exceptions observed may be statistically explained by the magnitude of the mean squares of reciprocal effects and the corresponding mean squares of errors. Studies on cacao have demonstrated the minor importance of reciprocal effects on yield characters and its components (Baez 1984; Mora 1987). The absence of a reciprocal effect simplifies the breeder's work, since the parents may be used either as a male or a female parent.

Table 5 shows that there was no interaction of combining-ability effects with years. This constitutes a favorable factor for breeding to the extent that it expresses the relative stability of the effects analysed. In general, GCA × Years, SCA × Years, and RE × Years interactions were not detected for the five characteristics assessed. This result conforms with the absence of G × Y interaction observed in Table 2 and may be explained by

Table 4 Values of the mean squares of GCA, SCA, and RE of the residuals and the average squared effects (components) of GCA and SCA relating to five characteristics, assessed in 25 cacao genotypes (1986–1990)

Year	Source	*df*	MS				
			NHFP[a]	NCFP[b]	WHSP[c]	WHSF[d]	PDFP[e]
1986	GCA	4	830.867**	1 107.516**	9.798**	4 261.250**	3.163**
	SCA	10	649.527**	656.579**	10.275**	254.460**	1.079**
	RE	10	209.947	208.952	2.195	33.815	0.172
	Error	72	129.856	133.048	1.307	37.943	0.368
	Components						
	$(1/4)\sum g_i^2$		17.525	24.362	0.212	105.583	0.070
	$(1/10)\sum\sum s_{ij}^2$		129.918	130.883	2.242	54.129	0.177
1987	GCA	4	865.008**	923.398**	6.881**	5 028.594**	0.509*
	SCA	10	292.248**	301.198**	5.057**	324.034**	0.172
	RE	10	276.496**	277.659**	2.865**	25.423	0.199
	Error	72	85.409	85.924	0.769	56.778	0.187
	Components						
	$(1/4)\sum g_i^2$		19.490	20.937	0.153	124.295	0.008
	$(1/10)\sum\sum s_{ij}^2$		51.710	533.818	1.072	66.814	−0.003
1988	GCA	4	619.547**	766.000**	6.017**	3 343.250**	3.430**
	SCA	10	425.928**	445.880**	7.692**	267.407**	0.806**
	RE	10	155.272	164.842	1.929	18.705	0.220
	Error	72	92.036	94.788	1.056	42.750	0.223
	Components						
	$(1/4)\sum g_i^2$		13.188	16.780	0.124	82.513	0.080
	$(1/10)\sum\sum s_{ij}^2$		83.473	87.773	1.659	56.164	0.146
1989	GCA	4	581.039**	622.019**	6.496**	4 804.500**	0.454
	SCA	10	216.602**	230.038**	4.093**	262.959**	0.298
	RE	10	107.049	114.581	1.144	56.279	0.272
	Error	72	69.148	67.862	0.717	57.852	0.396
	Components						
	$(1/4)\sum g_i^2$		12.797	13.854	0.144	118.666	0.001
	$(1/10)\sum\sum s_{ij}^2$		36.863	40.544	0.844	51.277	0.024
1990	GCA	4	424.133**	636.117**	4.802**	4 723.500**	6.581**
	SCA	10	322.041**	385.193**	5.434**	214.960**	1.560
	RE	10	346.856	206.261*	1.325	75.165	1.422
	Error	72	89.745	98.958	0.895	62.391	0.899
	Components						
	$(1/4)\sum g_i^2$		8.360	13.429	0.098	116.528	0.142
	$(1/10)\sum\sum s_{ij}^2$		58.074	71.559	1.135	38.142	0.165

*, ** Significant at the 5% and 1% level of probability, respectively
[a] Number of healthy fruits per plants–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

Table 5 Summary of the joint analysis of variances from GCA, SCA and RE relating to five characteristics, assessed in 25 cacao genotypes (1986–1990)

Source	*df*	MS				
		NHFP[a]	NCFP[b]	WHSP[c]	WHSF[d]	PDFP[e]
Years (Y)	4	6 923.938**	6 548.750**	65.986**	1 387.750**	91.504**
GCA	4	2 929.336**	3 722.226**	30.026**	21 831.250**	7.916**
SCA	10	1 710.795**	1 822.685**	30.390**	1 163.374**	2.330**
RE	10	710.705**	799.541**	7.346**	112.376	0.751
GCA × Y	16	97.814	83.206	0.992	82.461	1.555**
SCA × Y	40	48.888	49.051	0.540	40.111	0.396
RE × Y	40	45.229	43.188	0.528	24.253	0.384
Pooled error	360	93.239	96.116	0.949	51.534	0.415
Mean		37.456	39.125	3.929	105.733	1.890
CV%		25.780	25.058	24.788	6.789	34.071

*, ** Significant at the 5% and 1% level of probability, respectively
[a] Number of healthy fruits per plants–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

the same factors already mentioned. To a certain extent, the stability of the combining-ability effects shown in this study demonstrates the efficiency of selecting parents in cacao at the most-advanced ages. Bartley (1970) proposed starting the selection of cacao trees from the 8th year of planting in order to combine the yields from several sucessive years and so minimise the annual effects.

The estimates of the effects of GCA associated with each parent (g_i) and their standard deviation (SD) in the combined years are shown in Table 6. The high values of g_i are due to the fact that a particular parent is much better or worse than the other parents. Such a parent may be richer or poorer in favorable alleles as compared with the average allelic frequency. Estimates of g_i were highly variable, and ranged from 3.1-times for PDFP, to 16.0-times for WHSF, of their respective SDs.

Cultivar CC 41 presented a high and positive g_i value for the number of healthy fruits (NHFP), also confirmed by the high g_i value for the number of collected fruits (NCFP) and by the low value for the percentage of diseased fruit (PDFP). This parent contributed, genetically, to an increment in the production of fruits per plant, consistent with the highest average production of the 5 years (41.8). Cultivar SIAL 169 followed the same pattern with regard to the same characteristics, though at a lower level than that of CC 41 (Table 6). On the other hand, CC 41 presented a g_i value which was also high, but negative, for the character WHSF. Thus, even though this parent imparted a higher production of fruit in the combinations in which it participated, the result was a lower final production due to the lower weight of the seed per fruit (95.0 g.fruit^{-1}). This was the worse performance among the five parents for the character in question.

An inverse situation occurred for parent ICS 1 (Table 6). The positive and high value of g_i for the character WHSF, and low and negative values for NHFP, NCFP and PDFP, revealed a significant contribution of this genotype to the increment in seed weight per fruit from a lower production of fruits. ICS 1 presented the highest seed weight per fruit (122.8 g.fruit^{-1}), as well as the highest seed weight per plant (4.3 kg.plant^{-1}), from the second lowest production of fruit (35.8). Pereira et al. (1987) have also stressed these characteristics of ICS 1 in other environments.

Among the parents of the Bahia selections (SIAL 169, CEPEC 1 and SIC 19), the first was superior to the others in NHFP, NCFP, WHSP and WHSF, considering both the values of g_i and of the means. The parent SIAL 169 showed good agreement between real production and seed weight per plant and per fruit (Table 6). These results are in agreement with the findings of Monteiro et al. (1985) who analysed the same diallel, increased by one more parent (IMC 67), according to Griffing's method 3, model I. This analysis involved only two characteristics and 3 years (1980, 1981, and 1982).

The estimates of the effects of SCA of combined years associated with each crossing (s_{ij}) are shown in Table 7. These estimates represent the deviation of a hybrid as compared with what would be expected based on the GCA of the parents. Thus, high SCA values indicate a behavior comparatively better or worse than that expected on the basis of the GCA of the parents. The estimated effects of s_{ij} were two and a half times greater than their respective SDs. The hybrid CC 41 × SIC 19 (15) showed the highest positive effect of s_{ij} for fruit production (NHFP and NCFP). This is the result of the parent CC 41 complementing the contribution of the cultivar SIC 19, and so leading to an increase in fruit

Table 6 Estimates of the effects of GCA (g_i), of means of the characters, the standard deviations of differences between two parents (SD), of combined years relating to five characteristics (1–5), assessed in five cacao genotypes (1986–1990)

Character	Genotype				
	CC 41 (1)	SIAL 169 (2)	CEPEC 1 (3)	ICS 1 (4)	SIC 19 (5)
NHFP[a]	4.351	1.857	−5.683	−1.636	1.111
Mean of character	41.807	39.313	31.773	35.820	38.567
SD ($g_i - g_j$)	2.276				
NHFP[b]	4.718	2.570	−6.289	−2.164	1.164
Mean of character	43.842	41.695	32.836	36.961	40.289
SD ($g_i - g_j$)	2.311				
WHSP[c]	0.037	0.207	−0.605	0.430	−0.068
Mean of character	3.966	4.137	3.324	4.360	3.861
SD ($g_i - g_j$)	0.229				
WHSF[d]	−10.711	−0.008	−1.269	17.139	−5.151
Mean of character	95.023	105.725	104.465	122.873	100.583
SD ($g_i - g_j$)	1.692				
PDFP[e]	0.081	0.294	−0.183	−0.178	−0.014
Mean of character	1.971	2.185	1.708	1.713	1.876
SD ($g_i - g_j$)	0.152				

[a] Number of healthy fruits per plant–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

Table 7 Estimates of effects of SCA (s_{ij}) and the standard deviations (SD) of effects of two hybrids with common and incommon parents, of combined years to five characteristics, assessed in 20 cacao hybrids (1986–1990)

Genotype	(ij)	SCA				
		NHFP[a]	NCFP[b]	WHSP[c]	WHSF[d]	PDFP[e]
CC 41 × SIAL 169	12	1.731	2.178	0.091	−0.827	−0.010
SIAL 169 × CC 41	21					
CC 41 × CEPEC 1	13	2.802	2.812	0.197	−1.460	−0.065
CEPEC 1 × CC 41	31					
CC 41 × ICS 1	14	2.415	2.231	0.371	1.127	−0.088
ICS 1 × CC 41	41					
CC 41 × SIC 19	15	6.957	7.719	0.724	4.542	0.318
SIC 19 × CC 41	51					
SIAL 169 × CEPEC 1	23	2.903	2.387	0.390	3.409	−0.298
CEPEC 1 × SIAL 169	32					
SIAL 169 × ICS 1	24	2.567	2.239	0.625	6.813	0.159
ICS 1 × SIAL 169	42					
SIAL 169 × SIC 19	25	−3.905	−4.154	−0.522	−3.301	−0.028
SIC 19 × SIAL 169	52					
CEPEC 1 × ICS 1	34	6.234	6.495	0.795	3.814	−0.042
ICS 1 × CEPEC 1	43					
CEPEC 1 × SIC 19	35	−3.339	−3.549	−0.332	−0.577	−0.138
SIC 19 × CEPEC 1	53					
ICS 1 × SIC 19	45	4.161	4.409	0.677	3.771	0.027
SIC 19 × ICS 1	54					
SD ($s_{ij} - s_{ik}$)		4.318	4.384	0.436	3.211	0.288
SD ($s_{ij} - s_{kl}$)		3.740	3.797	0.377	2.780	0.249

[a] Number of healthy fruits per plant–NHFP
[b] Number of collected fruits per plant–NCFP
[c] Weight of humid seeds per plant–WHSP
[d] Weight of humid seeds per fruit–WHSF
[e] Percentage of diseased fruits per plant–PDFP

production. It is noteworthy that the highest means were produced by hybrids in which at least one of the parents exhibited a positive and high effect of GCA, as in the case of CC 41.

The crosses involving parents SIAL 169, CC 41 and SIC 19 showed low, even negative, values of the SCA effects for the characteristics WHSP and WHSF. However, when combined with ICS 1, a high GCA parent, they showed positive SCA effects. The cross SIAL 169 × ICS 1 (24) was outstanding for the combination of WHSP and WHSF (5.6 kg.plant^{-1} and 129.3 g.fruit^{-1}, respectively, as shown in Table 1). Parent CEPEC 1 presented negative SCA effects in all of the crosses, relative to the PDFP, giving rise to the lowest mean for this charater. The GCA value shown by CEPEC 1 for this characteristic, was also, negative (Table 6). To a certain extent, this parent contributed to reducing the percentage of diseased fruit.

The diallel analysis by Griffing's method 1 also permits an investigation of the effect of the GCA of one parent with itself (s_{ii}). Cruz and Vencovsky (1989) dealt with the genetic meaning of this s_{ii} effect, considering the sign as well as the magnitude. These authors state that it is an estimator of varietal heterosis of a progenitor. The greater the absolute value of s_{ii}, the greater the genetic divergence of the parent in relation to other parents. Moreover, this parameter will be negative when the deviations of dominance are predominantly positive, and positive in a contrary situation. The s_{ii} values of the parents for the two characteristics of major importance in this study (NHFP and WHSF) showed high and negative values. The case of ICS 1 was especially relevant (− 15.386 and − 15.526, respectively, calculated from the Table 1).

Finally, it is necessary to caution that, although Griffing's methods are statistically perfect, the author does not refer to the utilization of selfed parents in such methods. In the present study, particularly, the inclusion of this type of parent did not result in alterations in the combining-ability effects. This was corroborated by the analysis of the same diallel in method 3 (data not shown). The explanation for this may be in the utilization of self-compatible forms, whose relative homozygosis make them less depressive parents as demonstrated by Bartley (1969, 1971); by Carletto et al. (1977) and Vello et al. (1969); and by Soria (1963) and Soria and Esquivel (1969) for the cultivars ICS 1, SIAL and Catongo, respectively. In cacao, inbreeding is restricted to self-compatible genotypes.

Conclusions

The genotypes assessed, consisting of five parent cultivars and their 20 hybrids, involving ten F_1s and ten reciprocal F_1s, presented significant differences from one another for the number of healthy and collected fruits per plant (NHFP and NCFP), the weight of humid seeds per plant (WHSP) and per fruit (WHSF), and the percentage of diseased fruit per plant (PDFP). These differences favor beeding, since genetic gains may be obtained by selecting superior genotypes. The absence of interaction of genotypes with years may be attributed to the mixing of genotypes, the stabilization of the competition between cacao trees, and the presence of the Bahia selections SIC 19, SIAL 169 and CEPEC 1, and of the introduced cultivars, in the diallel. These Bahia selections have demonstrated great local adaptability and relative uniformity. Under these conditions cacao breeders may select genotypes based on only a few years of observation.

The study also demonstrated the existence of variability for both general combining ability (GCA) and specific combining ability (SCA) effects. However, estimates of the average squared effects of SCA were higher than those of GCA for the characters NHFP, NCFP and WHSP. Therefore, for these characters, the non-additive genetic effects were predominant. On the other hand, the superiority of the estimates of the average squared effects of GCA over SCA for the character weight of humid seeds per fruit (WHSF), emphasized the importance of additive variance for this character.

Breeding methods which explore the additive portion of genetic variation should be used in obtaining productive cacao trees in terms of high seed weight. Under these circumstances, cultivars ICS 1, SIAL 169 and CEPEC 1 may represent segregant populations that facilitate selection for the character. On the other hand, the breeding strategies which explore non-additive portion of genetic variation will result in significant gains if practiced for the number of fruits and weight of seeds per plant.

The analysis of the interactions of the GCA and SCA effects with years showed that, for the conditions under which this study was conducted, the genotypes tested expressed relative stability over the 5 years of assessment. The stability of these effects makes possible the application of predictive composite techniques.

It seems reasonable, also, that the selection of cultivars in cacao be made based on GCA (g_i) effects. This strategy will better reflect the superiority of cultivar *i* as to allelic frequency. This thesis may be corroborated by observing the performance of cultivar ICS 1, with a high positive GCA estimate for the characters WHSP and WHSF. Thus, ICS 1 contributed to an increase in the average weight of humid seed per fruit and per plant in all of the combinations in which it participated. In addition, the highest averages of seed weight per plant and per fruit were provided by the combination SIAL 169 × ICS 1 and its reciprocal.

References

Atanda OA (1973) Heterosis in crosses of *Theobroma cacao*. Exp Agric 9:23–29

Atanda OA, Toxopeus H (1971) A proved case of heterosis in *Theobroma cacao* L. In: Proc 3rd Int Cocoa Res Conf, CRIN, Tafo, pp 545–551

Baez OL (1984) Herencia de ciertos caracteres de la semilla del cacao (*Theobroma cacao*). MS thesis. Universidad de Costa Rica, San Jose, Costa Rica

Baker RJ (1978) Issues in diallel analysis. Crop Sci 18:533–536

Bartley BGD (1969) Twenty years of cacao breeding at the Imperial College of Tropical Agriculture, Trinidad. In: Proc 2nd Int Cocoa Res Conf, CEPLAC, Itabuna, Brasil, pp 29–34

Bartley BGD (1970) Yield variation in the early productive years in trials with cacao (*Theobroma cacao* L.). Euphytica 19:199–206

Bartley BGD (1971) First generation inbreds as parents in hybrids of *Theobroma cacao* L. Trop Agric 48:79–84

Carletto GA, Garcia JR, Magalhães WS (1977) Evaluación de hibridos *y* líneas endocriadas de cacao en Bahia. In: Proc 5th Intl Cocoa Res Conf, CRIN, Ibadan, pp 106–109

Cruz CD, Vencovsky R (1989) Comparação de alguns métodos de análise dialélica. Braz J Genet 12:425–438

Engels JMH (1985) A systematic description of cacao clones. V. Quantitative genetic aspects of several fruit characters. Café Cacao Thé 29:3–10

Griffing B (1956) Concept of general and specific combining ability in relation to the diallel crossing system. Aust J Biol Sci 9:463–493

Mariano AH, Bartley BGD (1981) Comportamento das seleções baianas na produção de cacaueiro. In: Proc 7th Int Cocoa Res Conf, J de Lafforest and Transla-Inter, Douala, pp 527–533

Monteiro WR, Carletto GA, Bartley BGD (1985) Avaliação da capacidade combinatória de clones de cacaueiro. In: Proc 9th Int Cocoa Res Conf, Cocoa Producers' Alliance, Lomé, pp 227–232

Mora LGR (1987) Herencia de ciertos caracteres de la mazorca y del arvol de cacao (*Theobroma cacao*). MS thesis. Universidad de Costa Rica, San Jose, Costa Rica

Ojo AA (1982) A partial diallel evaluation of selected *Theobroma cacao* clones. In: Proc 8th Int Cocoa Res Conf, Cocoa Producers' Alliance, Cartagena, pp 667–671

Pardo J, Enriquez GA (1988) Herencia de algunos componentes de la calidad industrial en almendras de cacao (*Theobroma cacao*). In: Proc 10th Int Cocoa Res Conf, Cocoa Proceducers' Alliance, Santo Domingo, pp 695–699

Pereira MG, Carletto GA, Dias LAS (1987) Avaliação de híbridos de cacaueiros nas condições de Linhares-ES. Bol Técnico 150

Soria J (1963) Observaciones sobre las variedades y cultivares de cacao en Bahia, Brasil. Cacao 8:1–6

Soria J, Esquivel O (1969) Algunos resultados del programa de mejoramiento genetico de cacao en el IICA-Turrialba. In: Proc 2nd Int Cocoa Res Conf, CEPLAC, Itabuna, Brasil, pp 35–42

Soria J, Ocampo F, Paez G (1974) Parental influence of several cacao clones on the yield performance of their progenies. Turrialba 24:58–65

Sprague GF, Tatum LA (1942) General- vs specific-combining-ability in single crosses of corn. J Am Soc Agron 34:923–932

Tan GY (1990) Combining ability analysis of yield and its components in cacao. J Am Soc Hort Sci 115:509–512

Vello F, Mariano AH, Garcia JR, Nascimento TF, Magalhães WS (1969) O programa de melhoramento genético do cacau na Bahia. In: Proc. 2nd Int Cocoa Res Conf, CEPLAC, Itabuna, Brasil, pp 43–56

Vencovsky R, Barriga P (1992) Genética biométrica no fitome-lhoramento. RBG, Ribeirão Preto, São Paulo