Combining Ability Analysis of Yield and Its Components in Cacao

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Abstract. Six Trinitario females of cacao (*Theobroma cacao* L.) were crossed with nine Amazonian males in a factorial crossing design. The 54 hybrid progenies were used to estimate genetic variability due to general combining ability (GCA) and specific combining ability (SCA) for yield, pod production, pod weight, husk content, number of beans per pod, average bean weight, and pod value. The results demonstrated that GCA differed significantly for all characteristics from all three sources (i.e., female + male, female, and male). SCA (female x male) was also significantly different for all characteristics. The ratio of GCA to SCA ranged from 7.1 for number of beans per pod to 25.7 for pod weight. This result suggested that a major portion of the genetic variability was additive in nature for these characteristics. Among the six Trinitarios, KA2-106 was the best female parent; it contributed high yield and all the desirable pod and bean characteristics into the hybrid progenies. Trinitario KA2-101 combined high pod production and yield, but tended to transmit below-average pod and bean characteristics to its progenies. Amazonians KEE6 and KEE12 were the two highest-yielding male parents, but had below-average bean number per pod and average bean weight. KEE42 and KEE43 combined high yield and transmitted good pod and bean characteristics to their progenies. Based on the GCA effects and the mean performance of the hybrid progenies, a multi-line cultivar consisting of 20 high-yielding crosses with good pod and bean characteristics is being produced in seed gardens for commercial planting.

The ultimate objective of the Papua New Guinea cacao genetic improvement program is to develop hybrids that are high-yielding and combine desirable pod and bean characteristics. The choice of breeding method and parental germplasm to be used depends on the type of gene action and the extent of genetic variability available in the breeding population. The best method for estimating the breeding value of individuals is by studying their progenies. This method also is generally recognized as the most effective way to identify superior parents to be used for commercial hybrid seed production. With an effective crossing design, information is also provided for estimating general and specific combining abilities in the progenies produced from combinations of parental lines.

Combining ability is used to evaluate the performance of a selected line in combination with others. Sprague and Tatum (1942) defined general combining ability (GCA) as the average performance of a selected line in hybrid combinations and specific combining ability (SCA) as the performance of certain combinations that do relatively better or poorer than could be expected on the basis of the average performance of the lines involved. Combining ability has been studied on yield characteristics and pest and disease resistance in cacao (Gardella et al., 1982; Tan, 1987; Tan and Tan, 1988). Both GCA and SCA were reported to be important sources of variation in pod production (Ojo, 1982), but SCA was found to have no significant influence on average wet bean production per tree and per pod (Monteiro et al., 1984). Engels (1985) also reported that GCA was more important than SCA for number of seed per fruit, weight per seed, fruit wall thickness, and fruit length and diameter. Soria et al. (1974) reported highly significant differences between GCA of male and female parents, and SCA from

male x female interaction for wet bean production per tree. High heritabilities were also obtained from measurement on bean length and diameter, total weight, wet weight of bean, and number of beans (Soria et al., 1974). Since yield in cacao is a complex characteristic comprising various components, it is apparent that selection criteria, which include both yield component measurements and yield data, would result in a higher probability for selection advancement. Quantitative genetic studies on these characteristics of cacao are important (Kennedy et al., 1987). The objective of this study was to estimate the GCA and SCA for yield and its components from 54 hybrid progenies.

Materials and Methods

Papua New Guinea Trinitario cacao is descended from crosses between 'Criollo' and 'Foresterio' and is very heterogenous. The material was introduced by Germans from Samoa, Java, and Sri Lanka in the early 1900s. The six Trinitario female parents (K82, KA2-101, KA2-106, KA6-101, K24-102, and KT140) were among the best selections from the population. Amazonian seeds were introduced to the country from Trinidad in 1962-64. The nine Amazonian male parents (KEE5, KEE6, KEE12, KEE22, KEE23, KEE42, KEE43, KEE47, and KEE52) were derived from individual tree selection from field trials. The main characteristics of these two populations were described in detail by Wood and Lass (1985).

The factorial crossing design described as North Carolina Design II (Cornstock and Robinson, 1948) was adopted. All the resulting crosses were considered fixed effects. The 54 hybrid progenies were planted in the field in Nov. 1981 in a randomized complete-block design with four replications. Each plot consisted of 16 trees, planted in a 4-m² pattern (625 trees/ha). The entire experiment was surrounded by two or more guard rows. Maintenance treatments were applied uniformly to each tree as follows: 4 x 280 g/tree per year 15N-15P-15K fertilizer; canopy pruning for height control twice yearly; phytophthora pod rot control using metalaxyl in wet seasons, and weed control by a combination of herbicides and hand-slashing. Overhead canopy shade (*Gliricidia* spp.) was regulated to $\approx$ 10% to 20% light interception.

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Table 1. Means, ranges, and coefficients of variation for yield, pod, and bean characteristics of 54 hybrid cacao progenies from crosses involving six Trinitario lines used as female parents and nine Amazonian lines used as male parents.

Characteristics	Mean	Range	cv (%)
Pod weight (g)	614	424-855	12.2
Husk content (%)	68.4	61.4-74.4	4.1
Beans per pod (no.)	36.6	27.5-46.5	10.0
Bean dry weight (g)	1.46	1.15-1.77	7.9
Pod value	19.3	13.0-26.8	13.5
Pod production (no./tree per year)	119.6	72.4-193.0	14.7
Yield (kg·ha ⁻¹)	3339	1694-4642	18.9

Number of pods for each individual tree was recorded at fortnightly harvests. Yield components were determined on random samples from each plot. The dry cacao beans were prepared according to the normal procedure used by commercial plantations. Fermentation of the raw beans is required for the development of chocolate flavor of the beans. To keep the identification of each progeny, the sample was kept separately in nylon mesh bags and fermented within the bulk of commercial cacao in wooden boxes. Average bean weight was determined after being dried to constant weight. Other characteristics measured included pod weight, husk content (percentage based on fresh weight), and number of beans per pod for each progeny. Pod value was expressed as the number of pods required to produce 1 kg of dried bean: Pod value = 1000/(bean number × mean bean weight); weights in grams. Potential yield (kg·ha⁻¹·year⁻¹) for each hybrid progeny was estimated from pod production divided by pod value multiplied by 625 trees/ha and a correction factor 0.83 (Tan, 1990). The potential yield was recorded at maturity on 6-year-old trees.

Analysis of variance was performed to partition mean effects due to males (M) and females (F) and M × F interaction. Estimates of GCA effects of the females and males for the seven characteristics studied, SCA effects of the hybrid combinations for yield and their respective SES were calculated according to the method of Gerhold and Park (1986). Simple correlation coefficients were used to study the association between pairs of characters from this study.

Results and Discussion

Mean values of the 54 hybrids for yield, pod and bean characters, ranges of progeny means, and coefficient of variation for each of the seven characters are given in Table 1. Analysis of variance (ANOVA) revealed highly significant differences among the 54 hybrids' progenies for all characteristics (Table

2). The genotypic variation was further partitioned into those of GCA for female + male, female, and male, and the SCA for female × male interaction. The results showed that GCA estimates were significantly different for all characteristics for female + male, female, and male. SCAs were also significantly different for all characteristics.

The relative importance of additive and nonadditive genetic effects is indicated by the ratio of GCA and SCA, which ranged from 7.1 for number of beans per pod to 25.7 for pod weight. The GCA results would suggest that a significant portion of the total genetic variance was additive in nature, controlling not only yield but also pod and bean characteristics. However, the ANOVA clearly indicate that not all variation can be attributed to additive effects because SCAs differed significantly for all characteristics.

Estimates of GCA effects and their SES for yield, pod, and bean characteristics of Trinitario female and Amazonian male parents are presented in Table 3. In most cases, the estimates were large enough to exceed twice their respective SES. Among the six female parents, KA2-106 was the most promising line that contributed high yield and was a good combiner for all desirable pod and bean characteristics into all of its progenies. The high yield of KA2-101 was due principally to very high pod production, but tended to transmit below-average pod and bean characteristics to its progenies. K24-102 also had a positive GCA effect on yield, but produced hybrids with high husk content, few beans per pod, and below-average pod production. Among the nine Amazonian male parents, KEE42 and KEE43 combined both high yield and other desirable pod and bean characteristics in their hybrids. The other Amazonian selections (KEE6, KEE12, KEE22, and KEE23) had good GCA effects on yield, but were either average or below-average in pod and bean characteristics. The two standard Amazonians (KEE5 and KEE52), which have been used extensively for commercial seed production in Papua New Guinea (Tan, 1982), showed below-average pod production and yield.

Estimates of SCA effects and their SES from all hybrid combinations showed that 27 out of 54 hybrids exhibited positive SCA effects on yield (Table 4). In 18 cases, the estimates of the positive SCA effects were greater than twice their respective SES. Apparently, these high-yielding hybrids were produced from either both, or at least one, of the parents with good general combining abilities.

Simple correlation coefficients were calculated from all possible combinations to determine the association among characteristics (Table 5). Pod weight was positively associated with husk content, number of beans per pod, and bean weight, while it was negatively correlated with pod value and pod production.

Table 2. Analysis of variance for Yield, pod and bean characteristic of 54 hybrid cacao progenies, and ratio of general combining ability (GCA) to specific combining ability (SCA).

Source of variation	df	Mean squares for						
		Pod wt	Husk content	Beans/pod	Bean dry wt	Pod value	Pod production	Yield
Hybrids	53	55,689**	39.2**	82.9**	0.099**	44.9**	8,334**	3,035**
GCA (female + male)	13	202,810**	115.2**	236.4**	0.343**	137.5**	29,665**	9,048**
GCA (female)	5	84,490**	154.7**	113.4*	0.643**	91.1**	16,259**	10,515**
GCA (male)	8	276,760**	90.6**	313.4**	0.156**	166.6**	38,044**	8,190**
SCA (female × male)	40	7,875**	14.5**	33.0**	0.019**	14.7**	1,401**	1,081**
Error	159	563	8.0	13.4	0.013	6.9	800	597
GCA/SCA		25.7	7.9	7.1	18.0	9.3	21.1	8.3

*** Significant at $P = 0.05$ and 0.01 , respectively.

Table 3. Estimates of general combining ability effects (SES) for Trinitario female and Amazonian male parental lines of cacao for pod and bean characteristic and yield.

Parental lines	Pod wt (g)	Husk content (%)	Beans/pod (no.)	Bean dry wt (g)	Pod value ²	Pod production (no./tree per year)	Yield (kg·ha ⁻¹)
Trinitario female							
K82	-82 (5.0)	-0.4 (0.28)	2.3 (0.32)	-0.20 (0.12)	1.7 (0.28)	-3 (27)	-381 (68)
KA2-101	-18 (5.9)	0 (0.22)	-1.2 (0.35)	0 (0.008)	0.3 (0.20)	314 (26)	536 (60)
KA2-106	37 (7.8)	-3.1 (0.29)	1.9 (0.26)	0.14 (0.011)	-2.7 (0.18)	152 (38)	631 (63)
KA6-101	-3 (7.1)	-0.8 (0.24)	-1.7 (0.38)	0.05 (0.009)	0.2 (0.29)	-63 (10)	-17 (100)
K24-102	56 (7.7)	1.5 (0.30)	-1.6 (0.37)	0.13 (0.013)	-0.7 (0.31)	-96 (25)	22 (86)
KT140	11 (7.7)	2.9 (0.21)	0.1 (0.32)	-0.11 (0.010)	1.5 (0.19)	-302 (23)	-793 (44)
Amazonian male							
KEE5	-67 (7.9)	-1.1 (0.46)	-3.8 (0.41)	0.02 (0.015)	2.2 (0.37)	-257 (29)	-897 (83)
KEE6	-137 (6.2)	0.3 (0.20)	-2.8 (0.36)	-0.09 (0.012)	2.6 (0.30)	601 (37)	549 (78)
KEE12	-88 (9.6)	-2.7 (0.27)	-0.2 (0.36)	-0.12 (0.013)	1.5 (0.02)	601 (42)	835 (91)
KEE22	-70 (6.9)	-0.8 (0.33)	-2.4 (0.35)	-0.02 (0.012)	1.2 (0.02)	222 (33)	181 (79)
KEE23	-12 (6.5)	-0.3 (0.23)	-1.1 (0.35)	0 (0.013)	0.5 (0.31)	-28 (34)	-189 (83)
KEE42	151 (7.6)	-0.9 (0.28)	6.2 (0.42)	0.16 (0.013)	-4.8 (0.17)	-317 (19)	307 (71)
KEE43	66 (10.6)	-0.3 (0.39)	2.9 (0.52)	0.05 (0.014)	-2.2 (0.35)	-92 (47)	344 (93)
KEE47	-6 (9.9)	2.2 (0.24)	-3.4 (0.43)	-0.01 (0.011)	2.2 (0.36)	-195 (23)	-602 (58)
KEE52	168 (8.5)	3.9 (0.34)	4.2 (0.37)	0.03 (0.011)	-2.8 (0.02)	-531 (17)	-531 (49)

²Pod value = 1000/(bean no. × mean bean weight); weights in grams.

Table 4. Estimates of specific combining ability effects (SES) on yield of 54 hybrids in cacao involving six Trinitario female and nine Amazonian male parental lines.

Parental lines	Amazonian male parents								
	KEE5	KEE6	KEE12	KEE22	KEE23	KEE42	KEE43	KEE47	KEE52
Trinitario female parents									
K82	-381 (528)	-317 (267)	762 (142) ²	-504 (166)	-512 (114)	-229 (161) ²	229 (285) ²	-1170 (97)	-718 (105)
KA2-101	-603 (244)	1120 (268) ²	1032 (141) ²	1303 (200) ²	415 (130) ²	195 (38) ²	1277 (125) ²	-40 (106)	-693 (115)
KA2-106	274 (218) ²	459 (66) ²	1127 (307) ²	1129 (237) ²	-63 (55)	666 (102) ²	356 (90) ²	569 (190) ²	192 (132) ²
KA6-101	-1023 (84)	556 (101)	92 (277)	-396 (105)	444 (277)	552 (149) ²	92 (225)	-131 (149)	-318 (98)
K24-102	-1087 (198)	678 (174) ²	1284 (260) ²	305 (260)	-164 (333)	307 (317)	-128 (338)	-771 (60)	-260 (122)
KT140	-1644 (1090)	237 (122)	-143 (41)	-933 (59)	-1057 (176)	39 (65)	-119 (149)	-1454 (147)	-848 (55)

²Twenty matings selected for reproduction of a new high-yielding multiple line cultivar. The mating K82 × KEE42 was included for its disease resistance to black pod.

Table 5. Correlation coefficients among seven characters in cacao (df = 52).

Traits	Husk content	Beans/pod	Bean dry wt	Pod value	Pod production	Yield
Pod weight	0.36**	0.54**	0.75**	-0.80**	-0.63**	-0.07
Husk content		-0.17	0.12	0.09	-0.54**	-0.61**
Beans per pod			0.17	-0.77**	-0.25	0.24
Bean dry weight				-0.73**	-0.36**	0.18
Pod value					0.34**	-0.33**
Pod production						0.76**

**Significant at $P = 0.05$ or 0.01 , respectively.

Pod weight and yield were not correlated. Similar results were reported by Glendinning (1963).

Pod production and pod value are the two major components of cacao yield. Results showed that correlation between yield and pod production was much higher than those between yield and pod value, which suggested that pod production was of greater importance in determining yield than pod value. However, the limitations on increasing yield by selecting high pod production may well be explained by the accompanying relationship of a decreasing pod and bean weight and an increasing pod value. This result is to be expected, since number of beans per pod and bean dry weight are the two determinants of pod

value. There was no significant correlation between yield and these two components. The result agreed with previous reports (Engels, 1985; Toxopeus and Wessel, 1970) that bean weight was independent of number of beans per pod. Large beans were reportedly associated with high fat and less shell content (Soria et al., 1974; Toxopeus and Wessel, 1970).

Pod weight was positively correlated with number of beans per pod and bean weight, but showed no correlation with yield. The negative correlation between yield and husk content indicates that selection for high yield could simultaneously reduce the percentage of pod husk. If husk content could be lowered by breeding, labor cost on breaking pods could be reduced.

Therefore, it should not be necessary to have large pods to obtain the benefits of numerous heavy beans toward high yield—many thin-husked pods could achieve the same results.

The results clearly demonstrated the existence of large differences in combining ability for yield, pod, and bean characteristics. Although additive genetic effects are of major significance, there was also considerable genetic variability due to nonadditive effects. Based on GCA effects and the mean performance of the hybrids for their yield, pod, bean and disease-resistant characteristics, 20 specific crosses were considered promising (Table 4). A new cacao cultivar composed of these 20 high-yielding lines was reproduced in biparental seed gardens and was recommended to growers for commercial planting. The chance of recovering such recombinants with high yield and desirable pod and bean characteristics is high because both additive and nonadditive genetic variation were considered in the selection.

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Unreduced Pollen in a Wild Tetraploid Relative of Sweetpotato

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Abstract. Nonreduction of pollen mother cells was observed in a wild tetraploid morning-glory related to the sweetpotato (*Ipomoea batatas* L. Lam.). Techniques for identifying and determining the frequency of expression of the trait are straightforward. Previous strategies for transfer of germplasm from tetraploid ($2n = 4x = 60$) species to the hexaploid ($2n = 6x = 90$) sweetpotato involved crosses with diploids ($2n = 2x = 30$) to obtain triploids that then were doubled to $6x$. Nonreduction of pollen mother cells probably represents the natural mechanism for raising $4x$ to $6x$ since pollination of $2x$ ovules with unreduced pollen ($4x$) should give rise to $6x$ progeny without need for somatic doubling. Plants carrying this trait should be useful as bridging types for introgressing genes from wild $4x$ species into sweetpotato. A wide range in nonreduction (up to, 74%) was recovered in progeny of controlled crosses among selected plants, but data were not sufficient to estimate gene action.

During the past two decades there has been an increasing interest in the evolutionary origin of sweetpotato, a major food of the tropics that ranks seventh in carbohydrate production among the major world crops (FAO, 1981). Taxonomic relationships of *Ipomoea* section Batatas have recently been re-

viewed by Austin (1988), who concluded that *I. triloba* and *I. trifida* are the closest extant relatives of the sweetpotato. Shiotani (1988) has presented a review of the most recent phylogenetic studies in his discussion of genomic structure and gene flow in the section. Strategies for the use of exotic germplasm in sweetpotato breeding were recently summarized (Iwanaga, 1988). It is generally accepted that the sweetpotato originated in northwestern South America.

The sweetpotato is a hexaploid morning-glory with 90 somatic chromosomes and the related species are tetraploid ($2n = 60$) or diploid ($2n = 30$). Strategies in phylogenetic studies

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