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Reciprocal differences and combining ability for growth and yield components in cacao (*Theobroma cacao* L.): a case of recommended cacao varieties in Ghana

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Abstract The inappropriate use of cacao clones either as female or male parents in seed gardens have been suggested as some of the reasons for the low yields of cacao hybrid varieties grown in West Africa. The concept of reciprocal effects in cacao crosses has not been well studied. To investigate the impact of maternal effect on growth and yield traits, reciprocal differences and combining abilities of recommended cacao parents in Ghana were evaluated. Six clones, comprising four important seed gardens clones used across West Africa and two clones previously used as standards in international breeding projects were crossed in a 6 × 6 complete diallel mating design to produce 30 F1 progenies. These progenies were tested in the field using a random block design with four blocks and elementary plots containing 20 plants. Growth and yield traits including stem cross-sectional area in juvenile stage, jorquette height, bean weight, number of beans per pod and bean yield were monitored over a 6-year period. Mean squares of general combining ability (GCA), specific combining ability (SCA) and reciprocal effects were significant for almost all the traits except jorquette height in SCA. This indicates that additive and non-additive gene effects are important in the inheritance of the traits. The presence of reciprocal differences for all traits suggests the influence of maternal effects in controlling the traits. Manual pollinations for commercial seed production should, therefore, follow established protocol and clones recommended as female and male parents used strictly as recommended. One of the standard clones, AMAZ15/15 had significant positive GCA effect for yield, and consistently produced progenies with high SCA values. It could be added to parental clones currently used in producing cacao varieties in the seed gardens in Ghana and other West African cacao growing countries.

Keywords Bean weight · Diallel · General combining ability · Improved varieties · Specific combining ability

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Introduction

Cacao is a humid tropical crop grown in areas with high annual rainfall. The primary centre of origin is South America (Motamayor et al. 2008), but, because of its importance, it is now cultivated in most tropical regions. It is cultivated for its fruit, from which the seeds are used for the production of chocolates and confectionaries. Ghana is the second largest cacao producer in the world and the cultivation of the crop is estimated to employ about 800,000 household families (Ghana Cocoa Board 2019). The seed obtained from the cacao pod is a major contributor to Ghana gross domestic product (GDP), accounting for 8.2% of GDP and 30% of total export earnings in 2010 (Asante-Poku and Angelucci 2013).

Cacao cultivation in Ghana started in the second half of the 19th century, and its production spread rapidly across the forest regions. The cacao cultivars grown at that time were mainly of Amelonado origin, uniform in most of the economic traits and partially self-compatible (Posnette 1943). With the establishment of West Africa Cacao Research Institute in 1938 in Ghana, F1 seeds derived from 102 pods of cacao from Trinidad (Posnette 1951) were introduced to broaden the genetic base of cacao varieties being grown in West Africa. After field evaluation of the 102 pods, 11 open pollinated F2 seeds of predominantly Upper Amazon trees were selected and distributed to farmers in Ghana and other West African countries (Glendinning 1957). Further research by the British Research Team focused mainly on estimating the combining abilities of introduced clones in crosses with the local selections for vigor, yield and resistance to diseases (Glendinning 1964; Posnette 1951). Ten clones with good general combining ability for dry bean yield were selected as female clones, and the progeny derived from crosses with some local selections (generally referred to as Series II hybrids) were made available from the seed gardens to farmers (Glendinning 1966). Subsequent breeding efforts resulted in the development of three different groups of hybrid varieties (Modified Series II and Inter Amazon), which were also released to farmers (Edwin and Masters 2005).

Currently for commercial cacao production in most of the West African countries where the bulk of cacao is produced, farmers obtain recommended varieties from seed gardens established with mainly Upper Amazon clones previously tested for good combining ability for key agronomic traits (Edwin and Masters 2005; Tahi et al. 2019). Presently in Ghana, there are about 27 cacao seed garden stations being managed by the Seed Production Division of COCOBOD. Generally, each seed garden station is planted to between four and six parental clones which are used to generate hybrid seedlings and distributed to farmers. The parental clones are specified as either female or male parents at the time of establishment of the seed gardens, and seed pods are generated through manual pollination.

A major challenge to this system is that, sometimes the genetic purity of the seedlings produced does not conform to recommendations on manual pollination of seed garden parents (Padi et al. 2015). Moreover, there is no established seed quality monitoring mechanism and manual pollination to generate specific crosses for pod production is not always followed. The choice of the direction of crosses is therefore based on the self-incompatible of parents to avoid the diffusion of self-pollinated seeds and not on the differences in production between reciprocal crosses. Padi et al. (2016) studying the impact of cacao seed purity and genotype on seedling survival and precocity observed that parentage of unapproved crosses are among the recommended varieties supplied to farmers for commercial cacao planting. In one of the seed garden station, pollen contamination as a result of inappropriate cross pollinations and self-fertilization contributed to about 50% of seedlings produced. Lanaud et al. (2017) realised that self-incompatibility is not strict in cacao and there is the possibility that self-crosses occur even on self-incompatible clones. The high proportion of inappropriate cross pollinations and self-fertilization in most seed garden station may partially explain the low average yields of 400–450 kg/ha on farmers' farms (Baah, et al. 2011), though on-station trials and on-farm demonstrations have recorded dry bean yields in excess of 2000 kg/ha (Aneani and Ofori-Frimpong 2013).

In crops such as cacao where out-crossing is very high, it is crucial to know what influence the maternal genotype have on yields and other traits. Many studies have been conducted on maternal effects through the use of reciprocal mating designs (Satyavathi et al. 2016; Fan et al. 2014; Upadhyaya et al. 2010). If reciprocal effects are significant, then the differences can be ascribed to cytoplasmic sources which are contributed by the mother parent (Shen et al. 2015). Reciprocal differences persist in nature because the contributions of cytoplasmic determinants from male and female gametes to the zygote are not equal (Satyavathi et al. 2016). In maize, Mahgoub (2011) and Yao et al. (2013) indicated that reciprocal differences strongly influenced hybrid yield performance. For reciprocal application, selective mating design such as diallel has been used for the genetic improvement of many crops.

Currently, very few studies on diallel analysis have been carried out in cacao even though in addition to estimating general and specific combining ability effects, the model is able to clearly explain reciprocal effects. Lockwood (1981) in studying the inheritance of cocoa swollen-shoot virus disease in cacao seedlings revealed significant maternal effects with little evidence of specific reciprocal differences. Cilas et al. (1988) in 8 × 8 mating diallel design observed significant maternal effects on collar diameter growth in cocoa trees. Dias and Kagayama (1995) observed non-significant reciprocal differences for yield component in a 5 × 5 diallel analysis among Amazon and Trinitario clones. In a genetic analysis of resistance of cacao to black pod infection under laboratory conditions, Tahi et al. (2006) observed non-significant reciprocal effects for black pod infection. Nyadanu et al. (2017) in a genetic analysis of a 6 × 6 diallel crosses observed significant reciprocal differences for stem canker resistance.

Cocoa, as is the case in many other tree crops, is difficult to evaluate because large resources of land and labor are required across a long cultivation period. To minimize the long evaluation period, key agronomic traits including juvenile growth traits (plant jorquette height and trunk cross-sectional area) have gained interest in selecting high and early yielding genotypes (Daymond et al. 2002; Padi et al. 2012; Ofori et al. 2015; Padi et al. 2016). The trunk cross-sectional area represents the intensity of vegetative growth and provides an estimate of tree vigor and yield (Nesme et al. 2005). Also at a given planting density, cacao progenies that do not grow too tall or too short are preferred for establishing commercial plantations. This is because they facilitate crop management operations such as pruning, application of fertilizers and harvesting.

In Ghana and most of West Africa where cacao hybrids produced in the seed gardens do not conform to recommendations on direction of crossing (designated female and male recommended parents) during manual pollination, it is important to comprehensively evaluate the influence of maternal effects on the growth and yield performance of seed garden varieties. This paper therefore emphasizes the importance of maternal effects in cacao. It demonstrates that in addition to the requirement of self-incompatibility of the female parent, the choice of the crossing direction must be based on the performance of the crosses. Progenies derived from a 6 × 6 diallel mating design, with four of the clones used currently as seed garden parents and two standard clones used in international breeding project were studied. Expanding knowledge on how maternal parent in reciprocal crosses influences growth and yield traits is necessary for the cacao industry in West Ghana. This information is important to assure that the genetic purity of the seedlings produced is in conformity with recommendations on manual pollination of seed garden parent trees in Ghana. This will further guide the seed production division whether to invest more or otherwise on manual pollination to generate specific crosses recommended for pod production in Ghana.

Materials and methods

Plant materials

The study utilized cacao varieties derived from manual pollinations made from June to July 2011 between six clones (Table 1) using a diallel mating design without selfing. The six produced 15 direct F1 and 15 reciprocal F1 crosses (30 total crosses) according to Griffing's Method 3 (Table 2). The parental clones were AMAZ 15/15, PA 13, PA 150, PA 7/808, Pound 7 and T60/887. Except AMAZ 15/15 and PA 13 that have previously been used as standards in international breeding projects (Eskes 2011), these are important clones used as parents in the seed gardens across West Africa. AMAZ 15/15 is a clone of Iquitos origin, Pound 7 is of Nanay origin whereas clones with the prefix PA are of Parinari origin, belonging to the Marañón genetic group (Motamayor et al. 2008). T60/887 was derived from PA 7 × NA 32 made in Trinidad and collected by Posnette in 1944 (Lockwood and Gyamfi 1979).

Field evaluation and plant culture

Field experiments were conducted at Cocoa Research Institute of Ghana (CRIG), Tafo (a humid rainforest belt, latitude 06° 13′ N, longitude 0° 22′ W). Six-month old seedlings of the 30 progenies were transplanted in June, 2012 at a spacing of 2.5 m × 2.5 m (1600 plants/ha). Each plot consisted of 20 plants in a randomized complete block with four replicates to obtain 80 plants per progeny. In July 2012, each cacao seedling was fertilized with 70 g nitrogen supplied as ammonium sulphate. No agrochemical was applied

Table 1 Characteristics of the parents used for the study

Parental clone	Genetic type	Utilizations
AMAZ 15/15	Iquitos	Standard clone used in international breeding project[a]
PA 7/808	Parinari	New seed garden clone
PA 13	Marañón	Standard clone used in international breeding project[a]
PA 150	Parinari	New seed garden clone
Pound 7	Naney	Old seed garden clone
T60/887	Parinari × Nanay	Old seed garden clone

[a]Eskes (2011)

Table 2 Scheme of complete full diallel mating design without parents, with 30 cacao progenies

Parental	AMAZ 15/15	PA 13	PA 150	PA 7/808	Pound 7	T60/887
AMAZ 15/15		+	+	+	+	+
PA 13	+		+	+	+	+
PA 150	+	+		+	+	+
PA 7/808	+	+	+		+	+
Pound 7	+	+	+	+		+
T60/887	+	+	+	+	+	

thereafter for the first 24 months after planting. Following the start of flower production, application of fertilizers and agro-pesticides was carried out in accordance with recommended practices for cacao production in Ghana.

Data collection

Traits evaluated in this study were trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height, bean weight, number of beans per pod and bean yield (kg ha^{-1}). Data on Stem diameter of each seedling was measured 15 cm above-ground surface with the aid of electronic calipers every 6 months from September 2012 to March 2018. The trunk cross-sectional area in the juvenile stage was estimated from September 2012 to September 2015 stem diameter measurements. For jorquette height, distance from ground to point of jorquette, was measured with a meter rule 24 months after transplanting. Annual dry bean yields were estimated from the total number of healthy pods produced per plot (typically in four separate annual harvests) divided by the pod index. The pod index was obtained from the number of pods required to obtain 1 kg of dry cacao beans, estimated from the dry weight of a sample of 30 pods per plot. Bean yield records were obtained from October 2014 to March 2018.

Statistical analysis

For stastitical analysis, diversty among parental clones was estimated using principal coordinate analysis (PCoA) on the six parental clones to observe the pattern of genetic relatedness between them with the Past 3 software (Hammer et al. 2001). Pairwise Euclidean distances were calculated on 110 single nucleotide polymorphism (SNP) marker data, which was used to conduct the PCoA using a covariance matrix with data standardization option. The agronomic data was analysed for each trait using GenStat statistical software version 11(VSN International Ltd., Hemel Hempstead, UK). The average trait values, with progenies considered fixed was computed for each trait using a random effect model. Normality of each data was checked based on the plot of the residuals. For genetic analysis, mean squares of general combining ability (GCA), specific combining ability (SCA) and reciprocals difference were carried out using the procedure described by Griffings (1956), method III, fixed model. The model was as follows:

$$Y_{ijk} = \mu + l_k + g_i + g_j + s_{ij} + r_{ij} + e_{ijk}$$

where Y_{ijk} is the value of the character measured on cross i × j in the kth replication, μ is the population mean effect, l_k is the replication effect, g_i is the GCA effect of the ith parent, g_j is the GCA effect of the jth parent, s_{ij} is the SCA effect of cross i × j, and eijk is the environmental effect peculiar to (ijk)th individual. The additive variance (σ^2A), dominance variance (σ^2D) and environmental variance (σ^2E) were computed using, respectively, the mean squares GCA (σ^2f), SCA (σ^2fxm) and error (σ^2e) and determined, respectively, as follows: $\sigma^2A = 4(\sigma^2f + \sigma^2m)/2$, $\sigma^2D = 4(\sigma^2fxm)$ and $\sigma^2E = \sigma^2e$.Narrow-sense heritability (h^2ns) and broad-sense heritability (h^2bs) estimates were calculated as:

$$h^2ns = (\sigma^2A)/(\sigma^2A + \sigma^2D + \sigma^2E)$$

$$h^2bs = (\sigma^2A + \sigma^2D)/(\sigma^2A + \sigma^2D + \sigma^2E)$$

The relative importance of GCA and SCA was estimated using the general predicted ratio (GPR) for the traits as follows: GCA/SCA = (2MSgca)/(2MSgca + MSsca) (Baker 1978). The effect of SCA on parental mean performance was investigated. Pearson's correlation coefficients among the evaluated traits were also estimated per elementary plot and classified as weak (− 0.30 to 0.30), moderate (− 0.5 to − 0.3 and 0.30 to 0.50), strong (− 0.9 to − 0.5 and 0.50 to 0.90) and very strong (− 1.0 to − 0.9 and 0.90 to1.0) (Cohen 1992).

Results

Parental diversity and agronomic F1 progenies

The first two principal coordinates explained 62.1% of the total variation (Fig. 1). The two-dimensional diagram discriminated the parental clones based on the genetic distances among them. AMAZ 15/15, a clone of Iquitos origin and Pound 7 a Nanay origin were widely separated from the other clones and identified in two different quadrants. The four other clones (PA 13, PA 150, PA 7/808 and T60/887) which are all of Parinari origin had two each clustered in the same quadrant but widely separated. Analysis of variance of the 30 F1 hybrid progenies showed highly significant differences for all the traits (Table 3). Increase in trunk cross-sectional area in the juvenile stage (TCSAj) ranged from 70.36 cm^2 in progeny PA 13 × AMAZ 15/15–92.03 cm^2 in progeny PA7/808 × T60/887. Progenies with the smallest increment were dominated by those with AMAZ 15/15 parent, whereas the progenies with the largest increments were typically those with T60/887. For jorquette height, progenies with the highest jorquette height were dominated by those with AMAZ 15/15, whereas those with the lowest jorquette height were mainly those with PA7/808. Progenies derived from AMAZ 15/15 parents compensate stem growth with height. Two of the progenies (PA150 × PA7/808 and PA 13 × Pound 7) with significant ($p < 0.05$) reciprocal differences were lower than the best progeny PA7/808 × T60/887 for jorquette height. Bean weight varied from 1.12 g for progeny PA150 × PA7/808 to 1.39 g for AMAZ 15/15 × Pound 7, with a mean of 1.27 g. The best progeny for bean weight was significantly ($p < 0.05$) different from six out of the 15 reciprocal crosses. Progenies with the largest bean weight were dominated by those with AMAZ

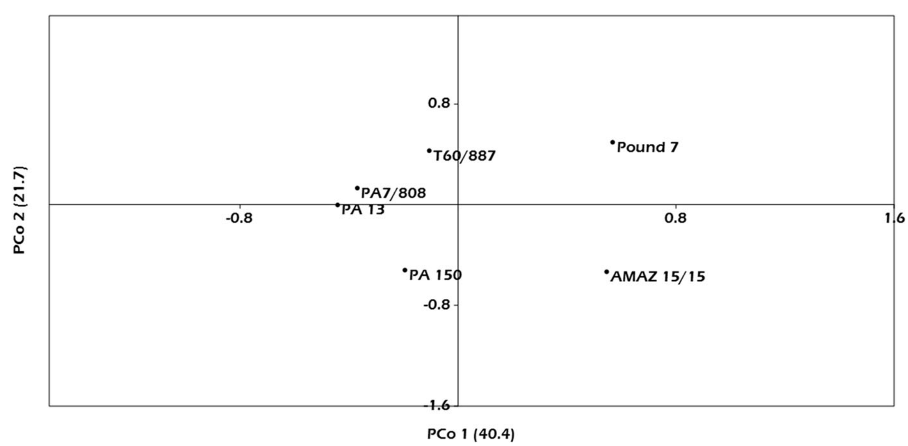

Fig. 1 Principal coordinate (PCo) plot of six cacao parental clones genotyped at 110 single nucleotide polymorphism (SNP) loci, used in a diallel mating design to generate 15 direct and 15 reciprocal F1 crosses (30 total crosses)

Table 3 Mean performance for increase in trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) of 30 cacao progenies, evaluated over 6-year period in Ghana

Crosses	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN	ABY(kg ha^{-1})
AMAZ 15/15 × PA 13	81.21b–i	176.2a–b	1.29b–g	39.19a–c	1148.1b–d
AMAZ 15/15 × PA 150	77.13g–k	163.6c–g	1.26c–h	42.35a	1174.4a–c
AMAZ 15/15 × PA7/808	81.04c–i	166.1b–e	1.23e–i	38.47a–e	821.6h–k
AMAZ 15/15 × PD 7	75.9i–k	168.7a–c	1.39a	42.35a	892.6f–i
AMAZ 15/15 × T60/887	72.21k–l	162.6c–g	1.33a–c	36.35b–g	654.3k–m
PA 13 × AMAZ 15/15	70.36l	165.2c–f	1.33a–c	33.31f–m	806.1i–l
PA 13 × PA 150	76.7g–k	161.3c–h	1.17i–k	28.77n	819.9h–l
PA 13 × PA 7/808	79.35e–j	166.9b–e	1.22f–j	34.56d–k	811.8i–l
PA 13 × Pound 7	76.47h–k	153.4g–k	1.23e–i	29.22m–n	544.0m
PA 13 × T60/887	83.43b–f	160.9c–i	1.34a–c	30.11l–n	1023.5c–f
PA 150 × PA 13	84.23b–e	155.4f–k	1.17i–k	33.49f–m	1042.1c–f
PA 150 × PA 7/808	75.33j–l	147.5j–k	1.12k	32.07g–n	630.8m
PA 150 × Pound 7	82.21b–g	154.1g–k	1.27c–h	36.72b–f	1002.4d–g
PA 150 × T60/887	80.36c–j	163.2c–g	1.26c–h	38.77a–d	923.1e–i
PA 150 × AMAZ 15/15	79.85d–j	159.6c–i	1.31a–e	34.83c–j	1004.3c–g
PA 7/808 × AMAZ 15/15	86.57a–b	162.5c–g	1.31a–e	31.73h–n	953.1e–i
PA 7/808 × PA 13	78.92e–j	151.9h–k	1.33a–c	31.55i–n	950.8e–i
PA 7/808 × PA 150	83.51b–f	163.2c–g	1.19h–k	34.05e–l	1220.3ab
PA 7/808 × Pound 7	78.08f–j	159.3c–i	1.14j–k	32.9f–n	802.8i–l
PA 7/808 × T60/887	92.03a	156.6e–j	1.3b–f	39.79a–b	1338a
Pound 7 × AMAZ 15/15	80.26d–j	161.6c–h	1.33a–c	36.01b–h	650.8l–m
Pound 7 × PA 7/808	82.72b–f	156.6e–j	1.37a–b	30.54j–n	852.6g–j
Pound 7 × PA 13	81.97b–h	167.4b–d	1.26c–h	34.45d–l	988.1d–h
Pound 7 × PA 150	84.91b–d	158.1d–i	1.24d–i	36.25b–g	910.9e–i
Pound 7 × T60/887	85.86b–c	177.9a	1.31a–e	39.46a–b	897.1f–i
T60/887 × PA 150	78.43f–j	156.8e–j	1.21g–j	35.65b–i	887.6f–i
T60/887 × AMAZ 15/15	78.94e–j	159.9c–i	1.31a–e	33.32f–m	683.6j–m
T60/887 × PA 13	85.21b–d	162.0c–h	1.24d–i	35.86b–i	873.9f–i
T60/887 × PA 7/808	81.9b–h	145.5k	1.31a–e	31.07j–n	1069.5b–e
T60/887 × Pound 7	81.62b–h	150.7i–k	1.32a–d	30.29k–n	835.9g–j
Mean	80.55	160.49	1.26	34.78	910.46
LSD (5%)†	5.5	10.4	0.08	4.4	170

Mean values with different alphabets within a column are significantly different at $p < 0.05$

†Least significant difference

15/15 parents, whereas the progenies with the smallest weight were typically those with PA 150. Number of beans per pod among the progenies ranged from 28 in progeny PA13 × T60/887 to 42 in progeny AMAZ 15/15 × PA 150, and were dominated by AMAZ 15/15 and PA 150 progenies. The bean yield among progenies varied more than twofold. The least yielding progeny was PA 13 × Pound 7 (544 kg ha^{-1}), with four other progenies having yields that were not significantly ($p > 0.05$) different. The highest yielding progeny PA7/808 × T60/887 (1338 kg ha^{-1}) was significantly ($p < 0.05$) different from its reciprocal cross T60/887 × PA7/808 (1069 kg ha^{-1}). Progenies with the highest bean yield were dominated by those with PA 150, whereas those with the lowest bean yield were mainly those with Pound 7.

Table 4 Analysis of variance of general combining ability (GCA), specific combining ability (SCA), reciprocal effect (REC) and genetic parameter estimates for in trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) of 30 cacao progenies derived from a 6 × 6 diallel mating design in Ghana

Sources	*d.f.*	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN	ABY(kg ha^{-1})
Progenies	29	77.71**	211.5**	0.018**	55.20**	143,347**
GCA	5	130.3**	333.57**	0.05**	85.74**	224,489**
SCA	9	55.2**	85.96	0.007*	28.10**	112,746**
REC	15	73.6**	246.00**	0.012**	61.20**	134,660**
Residual	87	25.45	54.81	0.0033	11.8	74,754
Genetic parameters						
σ^2A		10.72	35.39	0.006	8.23	15,963
σ^2D		29.8	31.1	0.0037	16.3	37,992
σ^2A/σ^2D		0.36	1.14	1.62	0.5	0.42
H^2		0.61	0.59	0.75	0.67	0.41
h^2ns		0.16	0.28	0.43	0.23	0.15

** = mean squares significant at $p < 0.01$, * = mean squares significant at $p < 0.05$, σ^2A = additive variance, σ^2D = dominance variance, h^2ns = narrow-sense heritability, H^2 = broad-sense heritability

Analysis of variance and genetic parameter estimates

Analysis of variance for combining ability showed that GCA and SCA variance were significant ($p < 0.05$) for the traits except for SCA for jorquette height (Table 4), suggesting that both additive and non-additive effects influenced the performance of the hybrid progenies. Reciprocal differences were significant ($p < 0.05$) for all evaluated traits. The additive variance component (GCA variance) was much larger than that due to the non-additive variance component (SCA variance) for jorquette height and bean weight. The reverse was observed for TCSAj, number of bean per pod and bean yield, where the non-additive variance component (SCA variance) was much larger than that due to the additive variance component (GCA variance). From the heritability estimates, narrow-sense heritability was generally low for all the traits, ranging from 0.15 for bean yield to 0.43 for bean weight. The broad-sense heritability was moderate to high, ranging from 0.59 for bean yield to 0.75 for bean weight.

GCA and SCA effects

Table 5 shows values of the general combining ability (GCA) estimates of the six parents. The parents with the highest positive values were T60/887 for TCSAj; AMAZ 15/15 for jorquatte height and bean weight; PA 7/808 for number of beans per pod; and PA 150 for bean yield. Parents T60/887 and Pound 7 contributed positive GCA effects to all the traits, except T60/887 for jorquette height and Pound 7 for bean weight. Parents PA 150, PA7/808 and AMAZ 15/15 had both positive and negative values, contributing differently for the different traits. Parents PA 13 contributed negative GCA effects to all the traits except for jorquette height.

Significant ($p < 0.05$) positive and negative SCA effects were observed for most traits (Table 6). Among the progenies, eight had significant SCA estimates for bean yield; with four being positive and four being negative. Seven had significant SCA estimates for TCSAj, with three being positive and the other four being negative. The best F1 progeny that reflected the highest positive values of SCA effects were: AMAZ 15/15 × PA 150 for bean yield; T60/887 × Pound 7 for jorquette height; AMAZ 15/15 × PA 7/808 for TCSAj; PA 7/808 × T60/887 for bean weight; and PA 13 × PA 7/808 number of beans per pod. Progenies PA 13 × T60/887, AMAZ 15/15 × PA13, AMAZ 15/15 × PA150, PA150 × Pound 7 and PA7/808 × T60/887 had positive SCA effects for all the traits except AMAZ 15/15 × PA150, PA150 × Pound7 and PA 7/

Table 5 General Combining Ability effects of parents for increase in in trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) evaluated over 6-year period in Ghana

parents	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN	ABY(kg ha^{-1})
AMAZ 15/15	− 2.15**	5.13**	0.040**	− 1.39*	18.95
PA 13	− 0.34	1.98	0.020*	− 1.16*	− 13.1
PA 150	− 0.98	− 2.76*	− 0.062**	0.64	36.8*
PA 7/808	1.11	− 3.60**	− 0.020*	2.51**	29.75
Pound 7	0.56	0.35	− 0.007	− 0.85	− 81.6**
T60/887	1.80*	− 1.09	0.029**	0.25	9.3
SE G(I)	0.63	1.19	0.009	0.51	17.9
SEG(I)-G(J)	1.36	3.7	0.027	1.56	55.7

*, **Significance when GCA effects were twice and thrice greater than S.E. (gi.), respectively

Table 6 Specific combining ability effects of 15 progenies for in trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) evaluated over 6-year period in Ghana

Progenies	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN	ABY(kg ha^{-1})
AMAZ 15/15 × PA 13	0.20	3.13	0.006	1.12	118.16**
AMAZ 15/15 × PA 150	1.07	− 1.29	0.026	0.66	154.44**
AMAZ 15/15 × PA 7/808	4.26**	2.28	− 0.027	− 0.80	− 39.46
AMAZ 15/15 × Pound 7	− 0.88	− 0.84	0.022	1.73*	− 8.34
AMAZ 15/15 × T60/887	− 4.64**	− 3.28	− 0.026	− 2.70**	− 72.93*
PA 13 × PA 150	1.24	− 1.35	− 0.023	− 2.13*	− 31.29
PA 13 × PA 7/808	− 2.19*	0.53	0.04	1.82*	− 224.79**
PA 13 × Pound 7	− 1.55	− 2.40	− 0.029*	− 0.49	− 41.47
PA 13 × T60/887	2.30*	0.09	0.007	− 0.32	27.55
PA 150 × PA 7/808	− 3.75**	1.24	− 0.027	− 0.98	− 104.66**
PA 150 × Pound 7	3.43**	− 1.99	0.028*	0.90	73.23*
PA 150 × T60/887	− 1.98	3.39	− 0.004	1.54	− 91.71*
PA 7/808 × Pound 7	− 1.82	0.69	− 0.014	− 1.83**	− 47.66
PA 7/808 × T60/887	3.50**	− 4.74*	0.029*	1.79*	264.71**
T60/887 × Pound 7	0.83	4.54*	− 0.006	− 0.31	24.25
SE G(I)	1.07	2.02	0.014	0.85	33.20
SEG(I)-G(J)	1.70	3.20	0.023	1.35	52.50

*, **Significance when SCA effects were twice and thrice greater than S.E. (gi.), respectively

808 × T60/887 for jorquette height and PA 13 × T60/887 for number of beans per pod. Crosses AMAZ 15/15 × T60/887, PA 13 × Pound 7 and PA 150 × PA 7/808 had negative SCA effects for all the traits. The SCA effects of the progenies (Table 6) for the various traits reflected closely the mean performance indicated in Table 3. Prediction of SCA values on progeny performance was highly efficient, with an $R^2 = 0.78$ for dry bean yield (Fig. 2). Progenies PA 7/808 × T60/887, AMAZ 15/15 × PA 150, AMAZ 15/15 × PA 13 × T60/887 and PA 150 × Pound 7 that had positive SCA effects for bean yield were similarly the best mean performance for bean yield. Likewise, crosses such as AMAZ 15/15 × PA 7/808, AMAZ 15/15 × T60/887, PA 13 × PA 150, PA 13 × PA 7/808, PA 13 × Pound 7, PA 150 × PA 7/808 and PA 7/808 × T60/887 which showed significant negative

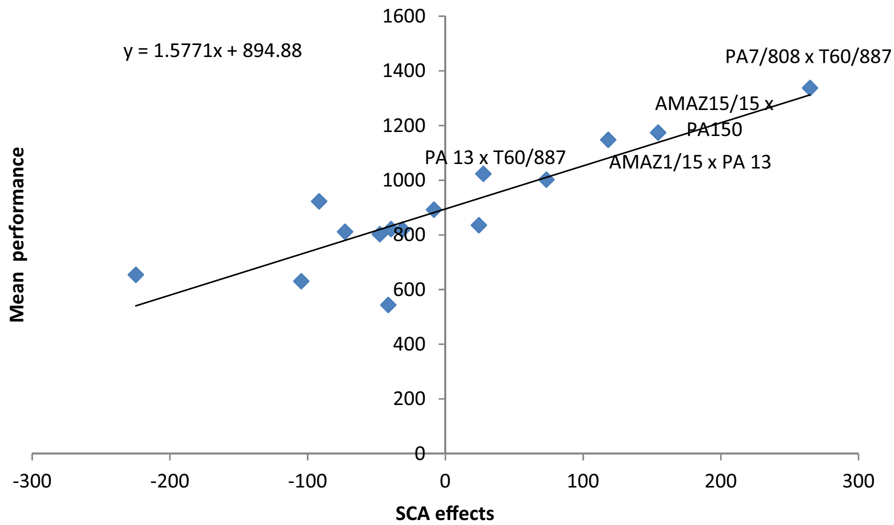

Fig. 2 Relationship between SCA effects and mean performance for bean yield. Note, deviations from the 1:1 line due in part to specific combining ability (SCA) effects

Table 7 Reciprocal effects of 15 progenies for trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) evaluated over six-year period in Ghana

Progenies	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN	ABY(kg ha^{-1})
PA 13 × AMAZ 15/15	− 2.94*	− 5.51*	0.02	− 2.94*	− 171.00**
PA 150 × AMAZ 15/15	1.36	− 2.00	0.03	− 3.76**	− 85.04
PA 7/808 × AMAZ 15/15	2.74	− 1.76	0.04*	− 3.37**	65.79
Pound 7 × AMAZ 15/15	2.18	− 3.51	− 0.03	− 3.17*	− 120.91**
T60/887 × AMAZ 15/15	3.37*	− 1.33	− 0.01	− 1.52	14.66
PA 150 × PA 13	3.77*	− 2.99	0.00	2.36*	111.10*
PA 7/808 × PA 13	− 0.72	− 7.51*	0.06**	− 1.50	69.50
Pound 7 × PA 13	2.75	7.03*	0.01	2.22*	222.03**
T60/887 × PA 13	0.89	0.55	− 0.05*	3.32*	− 74.79
PA 7/808 × PA 150	6.58**	7.83**	0.039	0.99	294.75**
Pound 7 × PA 150	1.35	2.00	− 0.01	− 0.24	− 45.74
T60/887 × PA 150	− 0.96	− 3.19	− 0.03	− 1.56	− 17.77
Pound 7 × PA 7/808	2.80*	− 1.36	0.12	− 1.18	24.92
T60/887 × PA 7/808	− 5.07**	− 5.59*	0.01	− 4.36**	− 134.25**
T60/887 × Pound 7	− 2.12	− 13.65	0.01	− 4.58**	− 30.60
REC(I)	1.39	2.60	0.02	1.11	42.9

*, **Significance when REC effects were twice and thrice greater than S.E. (gi.), respectively

SCA estimates correspondingly had lower bean yields (Table 7).

Reciprocal effects

Of the reciprocal effect (REC) estimates (Table 7), seven of the crosses had positive reciprocal effects with three (PA 150 × PA 13, Pound 7 × PA 13 and PA 7/808 × PA 150) being significant ($p < 0.05$) for bean yield. For TCSAj, ten of the crosses had positive reciprocal effects with four (Pound 7 × PA 7/808, T60/887 × AMAZ 15/15, PA 7/808 × PA 150 and PA150 × PA 13) being significant ($p < 0.05$). The reciprocal effects of progenies PA 150 × PA 13 and PA 7/808 × PA 150 were significant ($p < 0.05$) for the all traits studied except PA 7/808 × PA 150 for

Table 8 Pearson's coefficient of correlation among trunk cross-sectional area in the juvenile stage (TCSAj), jorquette height (JH), bean weight (BW), number of beans per pod (PN) and Average bean yield (ABY) of 30 cacao progenies evaluated

	TCSAj (cm^{-2})	JH (cm)	BW (g)	PN
JH (cm)	0.11			
BW (g)	0.16	0.17		
PN	0.13	0.56**	0.15	
ABY(kg ha^{-1})	0.64**	0.11	0.06	0.37*

**mean squares significant at $p < 0.01$; * = mean squares significant at $p < 0.05$

number of bean per pod and PA 150 × PA 13 for bean weight and jorquette height. Hybrid progenies PA 13 × AMAZ 15/15, PA 150 × AMAZ 15/15, T60/887 × PA 7/808, T60/887 × Pound 7, T60/887 × PA 150 and PA 7/808 × PA 150 had negative reciprocal effects for at least four of the traits.

Phenotypic correlations

The phenotypic correlations among all pairs of traits were positive (Table 8), ranging from r = 0.06 between bean weight and average bean yield to r = 0.64 between average bean weight and TCSA. Bean yield moderately (r = 0.37, $p \leq 0.05$) correlated with number of beans per pod but was not significant (r = 0.06) with bean weight, which indicates that yield components independently influence yield. Generally, bean weight weakly correlated with all the studied traits. Jorquette height positively correlated with number of beans per pod because of AMAZ 15/15 which impacts high jorquette height and number of beans per pod.

Discussion

Bi-clonal seed gardens in most cacao growing countries in West Africa have been established with Upper Amazon clones which are mainly self-incompatible. This ensures that harvested pods are generated through out-crossing to avoid self-pollinated seeds. The choice of the direction of crosses is therefore based on the self-incompatible characteristic but not on the differences in production between reciprocal crosses. This paper therefore emphasizes, first, the importance of maternal effects that requires that the choice of the crossing direction is based on the performance of the crosses and not solely on the self-incompatibility of the female parent and, secondly, the general and specific combining abilities for growth and yield performance of cacao varieties.

Variation in GCA and SCA

The experiment showed that genetic variance was attributable to both GCA and SCA, suggesting the importance of both additive and non-additive genetic effects in controlling traits. This confirms earlier findings by Cerventes-Martinez et al. (2006) on diseases and horticultural traits, Pereira et al. (2017) for physiological traits and Dias and Kagayama (1995) on yield traits that both GCA and SCA are important in controlling growth and yield traits in cacao. Selection methods that emphasize the use of both additive and non-additive effects are important in cacao breeding. This may be achieved by selecting parents that have good GCA effects and that, when crossed with specific parents, consistently produce families with high SCA values. The additive to dominance variance ratio that indicates the importance of additive effects showed that additive gene action was more important than non-additive variances for bean weight and jorquette height. This is an indication that the characters should respond favourably to direct selection, and selection based on parental performance would be an efficient way of predicting the performance of cacao progenies. This agrees with the high broad-sense heritability of 0.75 and narrow-sense heritability of 0.43 for bean weight which indicate the low difficulty in selection for bean weight and possibility of considerable gains in breeding programs.

The additive to dominance variance ratio that indicates the importance of non-additive effects of bean yield is in accordance with the low broad-sense heritability of 0.41 and narrow-sense heritability of 0.15 for bean yield, which indicate the difficulty in direct selection for bean yield. So, further yield improvement by selecting within this population is likely to be poor. As predicted by Fisher (1930) and supported by empirical studies (Karavolias et al. 2020), selection depletes the additive genetic variance as beneficial alleles becomes fixed after cycles of selection. Broadening the genetic base through crossing with clones from other genetic groups is likely to be of value to further yield improvement.

GCA effects

The GCA estimates for the entire traits were variable in magnitude and direction depending on the clone under study (Table 5). The significant positive effect of T60/887 for TCSAj; AMAZ 15/15 for jorquatte height and bean weight; PA7/808 for number of bean per pod; and PA 150 for bean yield is in agreement with the progeny mean performance, where progenies derived from T60/887 were associated with faster growth, those of AMAZ 15/15 with high jorquette height and PA 150 were typically those with highest bean yields. For the entire traits, parents T60/887, PA 7/808 and AMAZ 15/15 had more of the traits being positive for GCA effects. This indicates that those clones were good combiners for growth and yield traits and progenies derived from them would be characterized by high productivity. They should be used as parents in breeding programs that seeks to improve on yield and survival. Parents Pound 7 and PA 13 had negative GCA effects with Pound 7 being significant ($p < 0.01$) for bean yield and PA 13 for number of bean per pod. It could be concluded that these clones were of little use for the applied cacao breeding because they passed on a low productivity to their progenies. The high negative value of Pound 7 for bean yield indicates that this parent is not compatible with the seed garden parents, even though it has been in the seed garden for many years. Further genetic analysis of this parent in combination with clones other that those used in this study may be required to better inform on the relevance of Pound 7 and PA 13 parents in cacao breeding.

SCA effects

The experiment showed strong variation in specific combining ability (SCA) and the importance of specific cross combinations. Progenies PA 7/808 × T60/887, AMAZ 15/15 × PA 150, AMAZ 15/15 × PA 13 and PA 150 × Pound 7 recorded SCA estimates for yield traits. These progenies have much higher bean yield than that resulting from the sum of the GCA effects for their parental forms. Considering that the pedigree of the progenies include parents with a good general combining ability (PA 150, PA 7/808, T60/887 and AMAZ 15/15), the occurrence of interaction effects among these parents for yield is desirable. Further improvements in growth and yield traits can therefore be made by identifying specific high yielding crosses among good combiners. Parents of progenies PA 7/808 × T60/887 and PA 150 × Pound 7 are already used in the seed gardens for hybrid pod production across West Africa. However, crosses AMAZ 15/15 × PA 150, AMAZ 15/15 × PA 13 and PA 13 × T60/887 are potential hybrid candidates that could be exploited through multi-locational trials to determine their adaptation to different environments. The poor SCA effect of progenies AMAZ 15/15 × PA 7/808, AMAZ 15/15 × T60/887, PA 13 × PA 150, PA 13 × PA 7/808, PA 13 × Pound 7, PA 150 × PA 7/808 and T60/887 × PA 7/808 for bean yield indicate that these progenies are not useful for breeding programs that aim at developing progenies for high yield. This is not surprising because apart from progenies PA 150 × PA 7/808 and PA 7/808 × T60/887 both of which parents are already in the seed gardens, the rest had either PA 13 or AMAZ 15/15 as one of their parents. Parent PA 13 and AMAZ 15/15 are currently not seed garden materials but were previously used as standards in international breeding projects (Eskes 2011).

Reciprocal effects

The analysis of 15 direct and 15 reciprocal hybrid progenies in this study showed significant reciprocal differences, indicating maternal influence or role of maternal parents in controlling traits of economic importance in cacao. Similarly, significant maternal effects were reported by Cilas et al. (1988) on collar diameter growth in cocoa trees, Nyadanu et al. (2017) for stem canker resistance and Nyadanu et al. (2019) on leaf wax weight in cacao. The observed strong reciprocal effects for growth and yield traits in PA 7/808 × PA 150, Pound 7 × PA 13 as well as PA 150 × PA 13 requires that attention is placed on the direction of crosses in recommending cocoa varieties through the seed garden system. Additionally, it is important to include reciprocal crosses during experimental set-up in cacao breeding programs that seek to developed hybrid varieties to determine if a hybrid produced in one direction outperforms the reciprocal cross. In the present study, for example, the high bean yield of PA 7/808 × PA 150 would have been missed had reciprocal crosses not been included in the study.

Data from the present study clearly demonstrated that maternal effects have pronounced influence on dry bean yields in cacao. Also referred to as parent-of-origin, in most plants these differences are restricted to the endosperm which shows maternal expression (Köhler et al. 2012). In cacao, Boza et al. (2014) traced the maternal origin of CNN 51 variety using mitochondrial and chloroplast DNA. They reported that the maternal parent has the highest contribution to the overall genetic architecture. In this study, crosses involving AMAZ 15/15, PA 7/808, Pound 7 and PA 150 as females showed predominantly higher performance, demonstrating their maternal influence for the traits studied. All the hybrid progenies that were generated from AMAZ 15/15 and PA7/808 as female parents (except AMAZ 15/15 × T60/887 and PA 7/808 × Pound 7) had higher bean yields compared with their respective reciprocal crosses, with three being significantly ($p < 0.05$).

Similarly, crosses with PA 150 and Pound 7 showed positive cytoplasmic effects as maternal parents and should be exploited mainly as female parents in cacao variety development. For PA 13 and T60/887 crosses, they showed predominantly higher performance when used as males, indicating their paternal influence for the traits studied. These different expressions of maternal and paternal effects indicate that different organellar types may exist in cacao and clones possessing specific organelles may perform better as the male or the female. On the basis of these results, the selection and application of clones in variety development should strongly consider their use as either female or male parents. Similar to the results of the present study, Ofori et al. (2015) evaluating cacao progenies for cacao swollen shoot virus disease (CSSVD) resistance observed that clone T60/887 as female in a 3 × 8 NCII design had higher CSSVD severity score, indicating susceptibility but significantly ($p < 0.01$) low when used as male in a 6 × 3 NCII design, indicating resistance. In the same experiment, clone PA150 as female had low CSSVD severity score in the 3 × 8 NCII design but was high in the 6 × 3 NCII design.

Correlation estimates

The correlations between traits were generally low except for those between average bean weight and TCSA (r = 0.64, p = 0.01) and jorquette height and number of beans per pod (r = 0.56, p = 0.01) which were significant. Even for those significant, they were not large enough to ensure correlated response to selection, if selection were to be made on those traits with the highest heritability estimates. TCSA has been used as an indicator for selecting high-yielding cacao genotypes in later years (Glendinning 1964; Padi et al. 2012; Ofori et al. 2015; Padi et al. 2016). This concurred in this study as well, in that the correlation between TCSA in juvenile stage and bean yield was high (r = 0.64), explaining 40% of the variation. The observed poor correlation between the yield components (beans per pod and bean weight) concurs with what is generally known of yield component compensation in crop plants (Adams and Grafius 1971; Doaré et al. 2020). This weak correlation between the yield components agrees with previous studies (Cilas et al. 2010; Ofori et al. 2016, 2020). Jorquette height weakly correlated with other traits except number of beans per pod, and as such there would be the need to examine it in future studies to understand ways to exploit its positive correlation with number of beans per pod.

Conclusion

The significant reciprocal differences among the progenies identified for all the traits suggest that maternal influence is important. This implies that cacao clones should be tested extensively as either female or male i.e. both directions of crossing to ascertain the best way they can be applied in hybrid production to maximise yield. Reciprocal studies for yield traits in cacao is very scarce and previous studies have used factorial designs where several authors found additive component to be more important than non-additive component for yield (Soria et al. 1974; Tan 1990; Adomako et al. 1999). In such cases, crosses between groups of female and male parents which are self-incompatible to avoid the diffusion of self-pollinated seeds were recommended for seed production. The significant reciprocal effects and predominance of SCA in this study, indicates that bean yield was predominantly controlled by non-additive genes and strong maternal effects. Specific crosses with high performance should therefore be the focus of selection. From a commercial standpoint, pollinations in the seed gardens for hybrid pod production should conform to recommendations on direction of crosses where female parents are strictly used as females and male parents as male. This will ensure that the genetic integrity of the seedlings released to farmers is in conformity with performance of crosses recommended for production. Parental clones AMAZ 15/15 which is not a Seed Garden parent had significant positive GCA effect for the yield and growth traits and consistently produced progenies with high SCA values for most of the traits. Its addition as a parental clone to those currently used in producing cacao varieties in the seed gardens is recommended on the basis of the present observations.

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References

Adams MW, Grafius JE (1971) Yield component compensation—alternative interpretations. Crop Sci 11:33–35

Adomako B, Allen RC, Adu-Ampomah Y (1999) Combining abilities for yield and vegetative traits of Upper Amazon cocoa selections in Ghana. Plantations Recherché Dévelopement 6:183–189

Aneani F, Ofori-Frimpong K (2013) An analysis of yield gap and some factors of cocoa (*Theobroma cacao*) yields in Ghana. Sustain Agric Res 2:117–127

Asante-Poku A, Angelucci F (2013) Analysis of incentives and disincentives for cocoa in Ghana. Technical notes series. MAFAP, FAO, Rome

Baah F, Anchirinah V, Amon-Armah F (2011) Soil fertility management practices of cocoa farmers in the eastern region of Ghana. Agric Biol J N Am 2:174–181. https://doi.org/10.5251/abjna.2011.2.1.173.181

Baker RJ (1978) Issues in diallel analysis. Crop Sci 18:533–536. https://doi.org/10.2135/cropsci1978.0011183X001800040001x

Boza EJ, Motamayor JC, Amores FM, Cedeño-Amador S, Tondo CL, Livingstone DS, Schnell RJ, Gutiérrez OA (2014) Genetic characterization of the cacao cultivar CCN 51: its impact and significance on global cacao improvement and production. J Am Soc Hortic Sci 139:219–229

Cerventes-Martinez C, Brown JS, Schnell RJ, Phillips-Mora W, Takrama JF, Motamayor JC (2006) Combining ability for disease resistance, yield, and horticultural traits of cacao (*Theobroma cacao* L.) clones. J Am Soc Hortic Sci 131:231–241

Cilas C, Amefia YK, Bertrand B (1988) Etude de l'accroissement du diametre au collet dans un diallele quasi complet 8 × 8 chez le cacaoyer (*Theobroma cacao* L.). Café Cacao Thé 32:17–22

Cilas C, Machado R, Motamayor JC (2010) Relationship between several traits linked to sexual plant reproduction in *Theobroma cacao* L: number of ovules per ovary, number of seed per pod, and seed weight. Tree Genet Genomes 6:219–226

Cohen L (1992) Power primer. Psychol Bull 112:155–159

Daymond AJ, Hadley P, Machado RCR, Ng E (2002) Genetic variability in partitioning to the yield component of cacao (*Theobroma cacao* L.). Hortic Sci 37:799–801

Dias LAS, Kagayama PY (1995) Combining abilities for cocoa (*Theobroma Cacao* L.) yield component under South Bahia conditions. Theor Appl Genet 90:534–541

Doaré F, Ribeyre F, Cilas C (2020) Genetic and environmental links between traits of cocoa beans and pods clarify the phenotyping processes to be implemented. Sci Rep 10:9888. https://doi.org/10.1038/s41598-020-66969-9

Edwin J, Masters WA (2005) Genetic improvement and yields in Ghana. Exp Agric 41:1–13

Eskes AB (2011) Collaborative and participatory approaches to cocoa variety improvement. Final report of the CFC/ICCO/Bioversity project on Cocoa Productivity and quality improvement: a participatory approach (2004–2010). CFC, Amsterdam. The Netherlands/ICCO, London, UK/Biodiversity International, Rome, Italy

Fan XM, Zhang YD, Yao WH, Bi YQ, Liu L, Chen HM, Kang MS (2014) Reciprocal diallel crosses impact combining ability, variance estimation, and heterotic group classification. Crop Sci 54:89–97

Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford

Ghana Cocoa Board (2019) Cocoa. Ghana Cocoa Board. http://www.faostat/en/#data/QC

Glendinning DR (1957) The performance of the introductions and hybrids in W.A.C.R.I. trials. In: Report Cocoa conference 1957, Cocoa, Chocolate and Confectionery Alliance, London, pp 41–44

Glendinning DR (1964) A study of clonal cocoa varieties. Hortic Res 4:89–97

Glendinning DR (1966) Further developments in the breeding programme at the Cocoa Research Institute, Tafo. Ghn J Sci 6:52–62

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

Hammer O, Harper DAT, Ryan PD (2001) Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9–18

Karavolias NG, Greenberg AJ, Barrero LS, Maron LG, Shi Y, Monteverde E, Piñeros MA, McCouch SR (2020) Low additive genetic variation in a trait under selection in domesticated rice. G3 Genes Genomes Genet 10(7):2435–2443. https://doi.org/10.1534/g3.120.401194

Köhler C, Wolff P, Spillane C (2012) Epigenetic mechanisms underlying genomic imprinting in plants. Annu Rev Plant Biol 63:331–352

Lanaud C, Fouet O, Legavre T, Lopes UV, Sounigo O, Eyango MC, Mermaz B, da Silva MR, Loor Solorzano RG, Argout X, Gyapay G, Ebaiarrey HE, Colonges K, Sanier C, Rivallan R, Mastin G, Cryer N, Boccara M, Verdeil JL, Efombagn MIB, Peres Gramacho K, Clément D (2017) Deciphering the *Theobroma cacao* self-incompatibility system: from genomics to diagnostic markers for self-compatibility. J Exp Bot 68:4775–4790

Lockwood G (1981) Resistance of cocoa to swollen-shoot virus in Ghana II. Assessment of seed inoculation experiments. Ann Appl Biol 98:131–141

Lockwood G and Gyamfi MMO (1979) The CRIG cocoa germplasm collection with notes on codes used in the breeding programme at Tafo and elsewhere. Technical Bulletin, No. 10. Cocoa Research Institute of Ghana, Tafo

Mahgoub GMA (2011) Partitioning of general and specific combining ability effects for estimating maternal and reciprocal effects. J Agric Sci 3:213–221

Motamayor JC, Lachenaud P, Mota SJW, Loor R, Kuhn DN, Brown S, Schnell RJ (2008) Geographic and genetic population differentiation of the amazonian chocolate tree (*Theobroma cacao* L.). PLoS ONE 3:10

Nesme T, Plenet D, Hucbourg B, Fandos G, LauriI PE (2005) A set of vegetative morphological variables to objectively estimate apple (Malus × domestica) tree orchard vigour. Sci Hortic 106:76–90

Nyadanu D, Akromah R, Adomako B, Akrofi AY, Dzahini-Obiatey H, Lowor ST, Atta O, Kwoseh C, Awuah RT, Adu-Dapaah H, Larbi-Koranteng S, Adu Amoah R, Manigben KA, Attamah P (2017) Genetic control, combining ability and heritability of resistance to stem canker in cacao (*Theobroma cacao* L.). Euphytica 213:263. https://doi.org/10.1007/s10681-017-2059-1

Nyadanu D, Lowor ST, Akrofi AY, Adomako B, Dzahini-Obiatey H, Akromah R, Awuah RT, Kwoseh C, Adu-Amoah R, Kwarteng AO (2019) Mode of inheritance and combining ability studies on epicuticular waxvproduction in resistance to black pod disease in cacao (*Theobroma cacao* L.). Sci Hortic 243:34–40

Ofori A, Padi FK, Ameyaw GA, Dadzie AM, Lowor ST (2015) Genetic variation among cacao (*Theobroma cacao* L.) progenies for resistance to cacao swollen shoot virus disease in relation to total phenolic content. Plant Breed 134:477–484

Ofori A, Padi FK, Ansah FO, Akpertey A, Anim-Kwapong GJ (2016) Genetic variation for vigor and yield of cacao (*Theobroma cacao* L.) clones in Ghana. Sci Hortic 213:287–293

Ofori A, Padi FK, Amoako-Attah I (2020) Field evaluation of cacao progenies derived from Guiana clones for yield and black pod disease resistance. Crop Sci 60:249–262

Padi FK, Opoku SY, Adomako B, Adu-Ampomah Y (2012) Effectiveness of juvenile tree growth rate as an index for selecting high yielding cacao families. Sci Hortic 139:14–20

Padi FK, Ofori A, Takrama J, Djan E, Opoku SY, Dadzie MA, Bhattacharjee R, Motamayor JC, Zhang D (2015) The impact of SNP fingerprinting and parentage analysis on the effectiveness of variety recommendations in cacao. Tree Genet Genomes 11:44. https://doi.org/10.1007/s11295-015-0875-9

Padi FK, Ofori A, Arthur A (2016) Genetic variation and combining abilities for vigor and yield in a recurrent selection programme for cacao. J Agric Sci 155:444–464

Pereira AS, Almeida AAF, Branco MCS, Costa MGC, Ahnert D (2017) Combining ability, heritability and genotypic relations of different physiological traits in cacao hybrids. PLoS ONE 12(6):e0178790

Posnette AF (1943) Cocoa selection on the gold coast. Trop Agric (Trinidad) 20:149–155

Posnette AF (1951) Virus research at the West African cacao research Institute, Tafo, Gold Coast. Tropical Agriculture (Trinidad) 28:133–142

Satyavathi AV, Manga V, Muktinutalapati V, Rao S, Chittibabu M (2016) Genetic analysis of reciprocal differences in the inheritance of in vitro characters in pearl millet. Genet Mol Biol 39:54–61

Shen J, Dirks R, Havey MJ (2015) Diallel crossing among doubled haploids of cucumber reveals significant reciprocal-cross differences. J Am Soc Hort Sci 140:178–182

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

Tahi GM, Kebe BI, Goran JAK, Sangare A, Mondeil F, Cilas C, Eskes AB (2006) Expected selection efficiency for resistance to cacao pod rot (*Phytophthora palmivora*) comparing leaf disc inoculations with field observations. Euphytica 149:35–44

Tahi GM, Trebissou CI, Ribeyre F, Guiraud BSH, Pokou DN, da Cilas C (2019) Variation in yield over time in a cacao factorial mating design: changes in heritability and longitudinal data analyses over 13 consecutive years. Euphytica 215:106. https://doi.org/10.1007/s10681-019-2429-y

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

Upadhyaya HD, Sharma S, Singh S, Singh M (2010) Inheritance of drought resistance related traits in two crosses of groundnut (*Arachis hypogaea* L.). Euphytica 177:55–66

Yao WH, Zhang YD, Kang MS, Chen HM, Liu L, Yu LJ, Fan XM (2013) Diallel analysis models: a comparison of certain genetic statistics. Crop Sci 53:1481–1490. https://doi.org/10.2135/cropsci2013.01.0027

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