Australian Journal of Crop Science AJCS

Aust J Crop Sci. 19(03):310-321 (2025) | https://doi.org/10.21475/ajcs.25.19.03.p308 ISSN:1835-2707

Yield efficiency analysis in a cocoa clonal orchard derived from reciprocal grafting

Esther Anokye* Stephen Y. Opoku and Francis K. Padi

Cocoa Research Institute of Ghana, New Tafo, Akim, Ghana

***Corresponding author: Esther Anokye**
ORCID: https://orcid.org/0000-0002-9196-1987

Received: 09/12/2024

Revised: 22/01/2025

Accepted: 18/02/2025

Abstract: Analysis of trunk cross-sectional area (TCSA) and yield components were conducted among six full-sib families, and among thirty-six clones established from reciprocal grafting using scions from ortet selection in the six families. The objective was to analyze how full-sib family traits impact rootstock and scion characteristics to attain high yield efficiency in grafted cacao orchards. The study included two experiments: experiment 1 had six cocoa genotypes tested as hybrids whereas experiment 2 involved evaluation of 36 rootstock/scion combinations derived from the six genotypes in the first experiment. Both experiments were laid out in RCBD with four replications. Stem diameter and yield data were measured over a 4-year period. Diallel analysis was effective in summarizing the relationship between the six genotypes, distinguishing among them either as effective rootstock and/or scion types. Significant general compatibility (GC) was observed for all traits studied, but specific compatibility was not significant for any trait. This suggests lack of interaction between rootstock and scion genotypes in the expression of the traits. Patterns of GC revealed the distinctive performance of CRG 0314, as being suitable both as a rootstock type and productive scion, reflecting the attributes of its full-sib counterpart. Two-way ANOVA similarly showed significant rootstock and scion main effects, but no significant interaction for any trait, emphasizing that a good rootstock would be suitable for any productive scion type. Clonal performance reflected full-sib family attributes. Full-sib family performance was evident in rootstock types particularly for TCSA, whereas the impact on scion was mostly for yield related traits. High yield efficiency was achieved by two pathways: scions of high yield potential on invigorating full-sib rootstock, or scions of high yield potential on low vigour rootstocks.

Keywords: General compatibility; specific compatibility; rootstock; scion; homografting; heterografting; ortet.
Abbreviations: TCSA_Trunk cross-sectional area; GC_general compatibility; SC_specific compatibility.

Introduction

A sharp drop in cocoa output from West Africa in the 2022/23 season resulted in the first quarter of 2024 witnessing the sharpest rise in world cocoa prices over the past ten decades. The price per ton was predicted to reach US $9,000 by the end of the first quarter of 2024, scaling numerous all-time highs (Bloomberg, 2024). Scanning the cocoa commodity price records revealed that on average cocoa bean prices have increased 166% and 189%, respectively, in the New York and London cocoa bean futures markets over the 12 months prior, and 221 and 223%, respectively, over the 18 months before March 2024 (Thomas, 2024; ICCO, 2024). The outlook for production remains dire, predicated largely on production practices that do not match prevailing environments and climate impacts. Coupled with severe disease prevalence, an El Nino weather phenomenon associated with rising temperatures and reduced humidity in West Africa is impairing yields (Tabe-Ojong et al., 2024). The price surge has derailed long-established cocoa trade mechanisms, and disrupted supply chains of chocolate-based products, with a ripple effect on cocoa value-chain sustainability. It is a generally held view that what will return prices to sustainable levels is production technologies that will spur significant increases in productivity per land area. Key among these is suitable genotypes matching the production environments.

West Africa provides about 67 % of global cocoa supplies, largely through seed-derived orchards established with seed supplied from Seed Gardens of selected clones. Clonal cocoa orchards have gained importance not only in the Seed Gardens, but also in commercial plantings that take advantage of the early yield, specific quality traits of bean size, and sensory parameters of clones that are difficult to maintain in the seed planted orchards (Herklots and Murray, 2005; Apshara, 2017; Armengot et al., 2023). Use of clones was also considered an antidote to the large tree-to-tree variation in seed-derived plantings (Sounigo et al., 2005). The focal traits of ease of establishment, precocity, large annual yields, and suitable bean size are the key productivity parameters that guide clonal selection in cocoa (Irizarry and Goenaga, 2000; Padi et al., 2013). Almost all the clonal cocoa orchards in West Africa are established exclusively by grafting. However, there have been limited efforts in identifying rootstocks matching specific scion genotypes for optimal inter-tree spacing, pod load, orchard management, and yield efficiency. Yield efficiency, the ratio of the quantum of harvested beans relative to the increase in vegetative biomass of a genotype within the same yield development period is the ultimate productivity trait for cocoa orchards (Daymond et al., 2002; Padi et al., 2012). Mechanistically, rootstock genotypes that induce smaller scion biomass with higher bean output could increase the productivity per cultivated area (Larsen et al., 1992; Lachenaud, 1995) and reduce the time devoted to management tasks such as pruning and harvesting activities.

When the cocoa germplasm in West Africa shifted from Amelonado to the more vigorous Upper Amazon group for ease of establishment on the increasingly fragile soils (Posnette, 1951; Glendinning, 1967), a change of planting recommendations from 2700 plants per hectare (Van Hall, 1932) to the present 1111 (Manu and Tetteh, 1987) was implemented in Ghana to accommodate the increased vigour. Improving yield efficiency of clonal orchards subsequently focused largely on the search for low vigour rootstocks in a bid to reduce the vigour of the introduced germplasm. Small-sized sib-families were conceived to have the ability to impart a small stature to scions grafted onto them, leading various researchers to investigate the use of dwarf mutants as rootstocks to increase yield efficiency (Murray and Cope, 1959; Efron et al., 2003a; Yin 2004). Researchers at the Cocoa Research Institute of Ghana relied on several dwarf, crinkled-leaf mutant genotypes in a bid to impart reduced vigour to increase yield efficiency (Adu-Ampomah et al., 2005). The results mirrored those of Murray and Cope (1959) who studied several dwarf genotypes of cocoa as rootstocks and concluded that the possibility of use of dwarfing rootstock to increase yield was precluded because ICS 45, the genotype with the most dwarfing effect, gave poor yields even with a potentially high yielding scion. The general conclusion from these studies on cocoa was that the yield on dwarf rootstock genotypes was extremely poor to compensate for the loss of vigour that could lead to increased yield efficiency (Yin 2004; Susilo et al., 2005).

Trunk cross-sectional area (TCSA) which provides integrative information about whole-tree vegetative biomass accumulation is the commonest variable used to estimate cumulative growth over long periods in tree species (Barden et al., 2002; Lachenaud et al., 2007; Reddy et al., 2003) and is often used as an estimate of cocoa tree vigour (Efron et al., 2003b; Padi et al., 2017b; Ofori et al., 2017). In cocoa, longer primary roots of sib-families used as rootstock were found to be a key determinant of the vigour inducing effect on the scion (Susilo et al., 2005). In other tree crops, the size controlling effect of different rootstock genotypes is known to be imparted by differences in hydraulic conductance, which was related to rootstock xylem vessel dimensions in peach (Tombesi et al., 2011) and apple (Cohen and Naor, 2002). A suitable rootstock genotype should impart rapid juvenile-stage vegetative growth, reduced vegetative growth in the pod-bearing stage, and high pod load (Padi et al., 2012) without reducing bean quality characteristics of a selected scion genotype. Therefore, though it is intuitive to speculate that rootstock genotypes that impart rapid vegetative growth rate to the scion and a slow biomass increase during reproduction would impart high yield efficiency, implicit evidence for this hypothesis is still lacking. Identifying such suitable rootstocks for scion genotypes selected for productivity gains remains an urgent sustainability objective.

To gain an understanding of full-sib progeny characteristics when used as rootstock or scion types, we adopted a full diallel grafting approach for genotypes derived from full-sib families with known vigour and yield potential as rootstock and/or scion types in developing test clones in the present study. In classical genetic analysis, the full diallel model enables the estimation of genetic variances from random individuals, and to estimate general and specific combining ability effects from the interaction of all set of fixed genotypes for selected traits, including self-genotypes and all reciprocals (Griffing, 1956). To estimate specific and general compatibility between rootstock and scion genotypes, we used the full diallel grafting approach to generate clones between six cocoa genotypes. The 36 rootstock–scion combinations included six homografts (self-genotypes) and 30 heterografts (reciprocal genotypes). The overall objective is to define the attributes of cocoa seedling families that suit selection as rootstocks for high yield efficiency in cocoa. Specifically, whether generally adapted cocoa families are available as rootstocks for specific scion genotypes, or significant rootstock × scion interactions would imply the need for specific rootstocks to be developed for productive scion genotypes.

Results

Seedling family performance for vegetative and yield traits

Compared to the trunk cross-sectional area (TCSA) at the end of the juvenile phase (at 30 months after transplanting, MAT), rank changes were evident among the families for the TCSA at the end of the yield recording period of 76 MAT (Table 1). Only CRG 0332 maintained its rank as the least vigorous progeny at both recording events. In general, various vigour classifications are discernable: CRG 0332 and CRG 0333 have slow increases in TCSA at both vegetative and reproductive phases; CRG 0347 and CRG 0537 have slow increases in juvenile TCSA but increase TCSA sharply during the pod bearing period; CRG 0312 and CRG 0314 are generally of high vigour, however, CRG 0314 accumulates TCSA very slowly during the reproductive period.

Differences between progenies in terms of yield during the four yield-recording years were large, with a five-fold difference between CRG 0314 (the highest yielder) and CRG 0332 (the least yielding) families. Significant differences were not observed for yield among the four other progenies. The progeny with the least average yield

Table 1. Increase in trunk cross-sectional area (TCSA) and yield components of six cocoa progeny families evaluated over a four-year bearing phase

Progeny	Juvenile TCSA (cm^2) at 30 MAT	TCSA (cm^2) at 76 MAT	Hundred bean weight (g)	Pod value	Yield (kg ha^{-1} $year^{-1}$)	Yield Efficiency (kg cm^{-2} $year^{-1}$)
CRG 0312	13.36	44.17	114.1	22.58	614	0.049
CRG 0314	17.25	40.59	121.9	20.96	1721	0.156
CRG 0332	5.79	25.26	144.0	21.21	330	0.049
CRG 0333	9.26	31.41	119.6	23.16	955	0.109
CRG 0347	7.06	39.86	129.0	24.48	709	0.065
CRG 0537	9.59	38.93	105.3	26.29	752	0.069
Mean	10.38	36.70	122.3	23.11	847	0.083
SED $_{(df = 10)}$	0.77**	3.16**	6.66**	1.25**	212.8**	0.02**

MAT = months after transplanting; ** Significant at P < 0.01.

Table 2. Effect of rootstock and scion on cocoa tree vigour and yield traits over all combinations for six cocoa genotypes used to develop 36 clones evaluated in a field experiment.

	Genotype	TCSAj (cm^2)	TCSAr (cm^2)	Hundred Bean weight (g)	Pod Value	Yield (kg ha^{-1} $year^{-1}$)	YE (kg cm^{-2} $year^{-1}$)
Rootstock (R)	CRG 0312	10.60[bc]‡	29.24 [bc]	120.00	23.22	939 [a]	0.124 [a]
	CRG 0314	13.02[a]	36.18 [a]	122.96	23.44	921 [a]	0.094 [bc]
	CRG 0332	8.65[d]	32.39 [b]	120.27	23.85	719 [b]	0.087 [c]
	CRG 0333	9.51[cd]	28.07[c]	119.08	23.89	781 [b]	0.109 [abc]
	CRG 0347	9.27[cd]	29.25 [bc]	116.03	24.75	767 [b]	0.103 [abc]
	CRG 0537	11.31[b]	31.67 [b]	122.40	23.40	958 [a]	0.114 [ab]
	Significance†	**	**	NS	NS	*	*
Scion (S)	CRG 0312	11.88[a]	34.20 [a]	110.88 [c]	23.60 [b]	670 [c]	0.078 [c]
	CRG 0314	11.18[ab]	32.18 [a]	118.03 [b]	22.10 [c]	1345 [a]	0.155 [a]
	CRG 0332	9.97[bc]	23.04 [b]	133.87 [a]	21.22 [c]	869 [b]	0.148 [a]
	CRG 0333	10.22[bc]	33.46 [a]	135.91 [a]	22.01 [c]	948 [b]	0.105 [b]
	CRG 0347	10.07[bc]	31.33 [a]	122.27 [b]	23.72 [b]	797 [c]	0.094 [bc]
	CRG 0537	9.04[c]	32.60 [a]	99.78 [d]	29.89 [a]	454 [d]	0.052 [d]
	Significance†	*	*	**	**	**	**
R x S		NS	NS	NS	NS	NS	NS

†Results of the two-way ANOVA (rootstock x scion). Significance of F-tests: NS, non-significant; *P < 0.05; **P < 0.01.
‡ Numbers followed by the same letters are not statistically different (Standard error of the difference, df = 105)

across the four recording years, CRG 0332, had the largest bean weight of 144 g per hundred beans. Though all progenies had dry bean weights meeting industry expectations of the minimum of 100 g per hundred beans, CRG 0537 had the least bean weight with a corresponding high number of pods to achieve a kilogram of dry beans (pod value).

Yield efficiency varied three-fold from 0.049 kg/cm^2/year in CRG 0312 and CRG 0332 to 0.156 kg/cm^2/year in CRG 0314. The families, CRG 0312 and CRG 0332 reflect two pathways to attaining a target yield efficiency in cocoa. Though CRG 0332 had average yield of only 50% that of CRG 0312, the low TCSA of CRG 0332 relative to CRG 0312 resulted in similar yield efficiency values (Table 1).

Rootstock and scion effects on TCSA and yield traits in the grafting experiment

Rootstock x scion interactions were not significant for any of the studied traits, requiring a focus on the main effects. Rootstock effects were significant for the two TCSA traits (P < 0.01), and for average yield and yield efficiency (P < 0.05), but not for bean weight and pod value (Table 2). At the end of the pre-bearing phase, CRG 0314 as rootstock imparted the highest vigour, with CRG 0332 recording the least vigour, though not significantly different from CRG 0333 and CRG 0347. In the pod bearing phase, CRG 0314 remained the genotype that imparted the highest vigour. Taken together, the six rootstock types delineate into two groups: CRG 0314, CRG 0312 and CRG 0537 rootstocks that impart high TCSA, and CRG 0332, CRG 0333 and CRG 0347 imparting low TCSA. This vigour classification had a direct association on yield, with the high-vigour group recording significantly higher average yield than the low-vigour group. Ranking for yield efficiency was less clear-cut, with CRG 0312 imparting the highest yield efficiency, and CRG 0332, the least (Table 2).

As scions, significant (P < 0.05) differences were recorded for all traits (Table 2). CRG 0332 had the least TCSA at both stages of recording, whereas CRG 0312 and CRG 0314 were among the largest plants. Bean weight was least in CRG 0537 with a corresponding high pod value. CRG 0332 and CRG 0333 had the largest beans and among those with low pod values. As with the seedling families, CRG 0314 had the highest dry bean yield and the highest yield efficiency. In contrast, CRG 0332 which had the least yield among the seedling families recorded a high yield as scion, with yield efficiency not significantly different from that of CRG 0314 on account of a very low TCSA. CRG 0537 recorded the least average yield and yield efficiency.

General and specific compatibility, and reciprocal effects of cocoa genotypes used as rootstock or scion for measured traits

Analyses following Griffing's method 1 model B revealed significant mean squares for clones, and general

Table 3. Mean squares from the 6 x 6 diallel analysis of cocoa genotypes used in rootstock x scion combinations.

Source of variation	Df	Mean squares† TCSAj	TCSAr	Pod value	Hundred Bean weight	Yield	Yield efficiency
Clones	35	16.16*	112.25*	39.25*	696.58*	386.65*	7.28*
GC	5	54.29*	222.49*	98.76*	1989.85*	1064.57*	10.26*
SC	15	4.28	39.47	9.29	32.92	52.50	1.80
Reciprocal	15	15.33*	148.28*	49.38*	929.16*	494.83*	11.76*
Maternal	5	31.27*	389.71*	133.16*	2705.15*	13397.83*	32.71*
Non Maternal	10	7.36	27.57	7.49	41.16	72.36	1.28
Residual	105	6.97	37.86	6.10	105.82	81635.07	1.64

†TCSA is the trunk cross-sectional area for juvenile(j) and reproductive(r) growth stages.

Table 4. General compatibility (GC) and rootstock effects of six cocoa genotypes for growth and yield traits, derived from diallel analyses following field evaluation of a 6 x 6 model of rootstock x scion grafting.

	Genotype	TCSAj†	TCSAr	HBW	PV	Yield	YE
GC	CRG 0312	0.85	0.59	-4.68*	-0.11	-42.66	-3.99
	CRG 0314	1.71*	3.05*	0.37	-1.02*	285.71*	19.04*
	CRG 0332	-1.08*	-3.42*	6.95*	-1.20*	-53.42	12.25
	CRG 0333	-0.53	-0.37	7.37*	-0.89*	17.25	1.665
	CRG 0347	-0.72	-0.84	-0.97	0.66	-65.42	-6.81
	CRG 0537	-0.22	1.00	-9.03*	2.56*	-141.46*	-22.15*
Maternal Effects	CRG 0312	-0.64	-2.48*	4.56*	-0.27	134.48*	23.276*
	CRG 0314	0.92*	2.00	2.47	0.66	-212.17*	-30.37*
	CRG 0332	-0.66	4.68*	-6.80*	1.33*	-75.21	-30.95*
	CRG 0333	-0.35	-2.69*	-8.42*	1.03*	-83.79	2.33
	CRG 0347	-0.40	-1.04	-3.12	0.47	-15.39	4.79
	CRG 0537	1.14*	-0.46	11.31*	-3.21*	252.08*	30.93*

* $P < 0.05$; †TCSA is the trunk cross-sectional area for juvenile(j) and reproductive(r) growth stages; PV is pod value, HBW is hundred bean weight; and YE is yield efficiency.

compatibility (GC) for all the studied traits, whereas the specific compatibility (SC) was not significant for any of the traits (Table 3). Also, the rootstock – scion reciprocal effects were significant for all traits measured, and further decomposition of the significant reciprocal effects led to significant maternal (or rootstock) effects, but not for non-maternal effects.

For the GC effect which reflects the average performance of a genotype as rootstock and scion in combination with the other genotypes, the contribution of CRG 0314 in increasing TCSA was evident by the significant positive effects for TCSA at both juvenile and pod-bearing phases, whereas CRG 0332 had significant negative effects at both stages (Table 4). For the pod value and bean weight being negatively correlated traits, genotypes with a positive GC effect for pod value and negative GC effect for bean weight would imply undesirable contribution to trait expression. CRG 0537 illustrates such a genotype, whereas CRG 0332 and CRG 0333 have GC effects reflecting contribution in the direction of improving the expression of the two traits. For dry bean yield and yield efficiency, only CRG 0314 and CRG 0537 had positive and negative contributions, respectively.

In this diallel grafting design, maternal effects reflect the contribution of a genotype when used as rootstock over all scion types relative to its contribution as scion on all rootstock types. The maternal effect is, therefore, a relative value of a genotype's contribution to the trait as a rootstock, and reversing the sign of the effect would represent the relative value as a scion. For TCSA, the genotypes exhibited inconsistency in their contributions between the juvenile and pod-bearing phases. In the juvenile phase, only CRG 0314 and CRG 0537 significantly impacted TCSA as rootstock types (Table 4). In the reproductive phase, CRG 0312 and CRG 0333 increased TCSA better as scion (negative sign), whereas CRG 0332 was better as a rootstock. For the two bean traits (pod value and bean weight), the sign directions show that CRG 0332 and CRG 0333 are better suited as scion types than as rootstock genotypes. CRG 0537 was particularly suitable for the two bean traits as a rootstock type. The expression for bean yield and yield efficiency was generally correlated, with CRG 0537 and CRG 0312 contributing positive effects as rootstock, whereas CRG 0314 was particularly a good scion for both yield and yield efficiency. CRG 0332, on account of its contribution to increasing TCSA during the pod bearing phase, led to poor yield efficiency as rootstock.

The reciprocal effect estimates provide a straightforward means to identify a good rootstock or a good scion in any varietal combination for a target trait (Table 5). Positive reciprocal effect estimates for a particular trait indicate that the genotype combination for rootstock and scion should be reversed for the desired expression of the trait (except traits such as pod value where lower values are preferred to higher values). To illustrate, the reciprocal effects for all yield related traits (pod value, bean weight, yield, and yield efficiency) associated with CRG 0537 (as rootstock) were significant with sign directions reflecting the suitability of this genotype as rootstock in clone development. Similarly, reciprocal effects for yield efficiency in combinations where CRG 0312 was used as a scion were generally positive, supporting the use of CRG 0312 as a rootstock to achieve high yield efficiency. Consistent with observations on their maternal effects, the reciprocal effect estimates for yield efficiency associated with CRG 0314 and CRG 0332 were significant

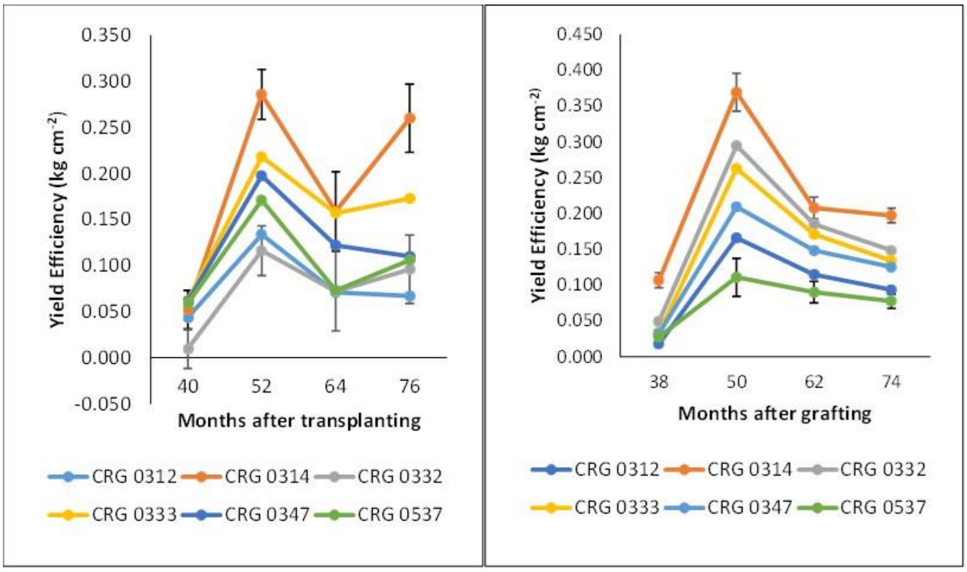

Fig 1. Yield efficiency of six cocoa genotypes in the first four years of the reproductive phase among (a) seed-derived genotypes (b) scion effect of clonal genotypes. The bars represent standard error of the means for each data collecting year.

with sign directions that indicate these are good scions for increasing yield efficiency in cocoa clones.

Individual clone performance for measured traits

Based on their progeny (family) performance, high yield efficiency in the clones was achieved either through a combination of two low-vigour genotypes (as measured by TCSA) or use of a high yielding scion genotype. This is exemplified by the two clones with the highest yield efficiency (Table 6): CRG 0312 / CRG 0314 having the highest yielding scion grafted on a high-vigour full-sib family, and CRG 0333 / CRG 0332 having two low-vigour genotypes. The 13 clones with yield efficiency above the mean were generally dominated by three scion types: CRG 0314 (five times), CRG 0332 (five times) and CRG 0333 (three times). This was reflected in the high yield expression of clones that had these three scions, making up 15 of the 17 highest yielding clones with yields above the mean. The impact of rootstock genotype on yield and yield efficiency is more nuanced. Aside CRG 0537 (as rootstock) which contributed to five of the 17 clones with yield above the mean, genotypes CRG 0312, CRG 0314 and CRG 0333 had three clones each among the high yielding set. For yield efficiency, however, CRG 0312 (high-vigour seedling family) and CRG 0333 (low-vigour) had the highest contribution of clones as rootstocks.

Examination of the individual clone performances reported in Table 6 reveals the loss of vigour, and yield of clones developed using CRG 0332 rootstock (the least vigorous full-sib family) relative to using the most vigorous full-sib family, CRG 0314, as rootstock. For the six scions, the relative loss of vigour in the pre-bearing phase (based on TCSA) from grafting on CRG 0332 relative to using CRG 0314 as rootstock was an average of 14%, with a range of 9% with CRG 0312 scion to 19% for CRG 0332 as scion. This translated into an average of 28% loss of yield with a range of 43% for scion CRG 0333 to 13% for CRG 0312. Yield losses resulting from reduced pre-bearing vigour of the rootstock was higher with the three productive scion types (CRG 0314, CRG 0333 and CRG 0332, 36% yield loss) compared with the three other scion types (CRG 0347, CRG 0312 and CRG 0537, 20% yield loss). The simple correlation coefficient between TCSAj and bean yield for each scion on the six rootstock types were for CRG 0314 ($r = 0.971$, $P = 0.001$); for CRG 0333 ($r = 0.902$, $P = 0.014$); for CRG 0332 ($r = 0.741$, $P = 0.092$), for CRG 0347 ($r = 0.548$, $p = 0.261$), for CRG 0537 ($r = 0.511$, $P = 0.300$) and CRG 0312 ($r = 0.409$, $P = 0.421$) attesting to the importance of rootstock vigour in expressing yield in the more productive scions.

Though not elaborated, homografting did not offer agronomic advantages to clone performance compared with heterografting for any of the measured traits: TCSAj (9.78 vs. 10.52 cm^2), TCSAr (31.53 vs. 31.05 cm^2), hundred bean weight (121.14 vs. 119.12 g), pod value (24.29 vs. 23.65), yield (0.84 vs. 0.85 t/year) and yield efficiency (0.10 vs. 0.11 kg/cm^2/year).

Family performance in relation to performance of descendant clones

Figure 1 illustrates the variation in yield efficiency among six progeny families (a) and clones (b) during the first four pod-bearing years. A biennial fluctuation of the yield efficiency is obvious, affecting all genotypes, and both seed-derived families and grafted materials. Based on the associated standard errors for the seedling families, CRG 0332, CRG 0312 and CRG 0537 had very low yield efficiencies, CRG 0347 as moderate, and CRG 0333 and CRG 0314 as having high yield efficiencies. The descendant scion, CRG 0314, derived from the seedling family maintained its high yield efficiency in the grafting experiment. Significant rank changes between the seedling family and clonal performance were evident for two genotypes: CRG 0332 and CRG 0537. Whereas the ortet selection (a tree selected from a family of seed origin from which clones are derived) from the family CRG 0332 (the worst performing seedling family for yield efficiency) improved significantly to become the second best among the clones due to improved clonal yield, the selection from the family CRG 0537 became the worst among the clones for yield efficiency.

Statistical significance of the slope of the seedling family – clone regression lines (Figure 2) indicates good prediction of clone performance from family TCSA in the juvenile phase ($P = 0.002$), pod value ($P = 0.019$) and dry bean yield ($P = 0.020$) but not for TCSA in the bearing

Table 5. Reciprocal effects of six cocoa genotypes derived from diallel analyses following field evaluation of a 6 x 6 model of rootstock x scion grafting.

Rootstock	Scion	TCSAj†	TCSAr	Pod value	Hundred Bean weight	Yield	Yield efficiency
CRG 0314	CRG 0312	-0.76	-3.88*	-1.87*	3.48*	437.56*	59.08*
CRG 0332	CRG 0312	-0.37	-8.63*	-0.77	7.74*	112.56*	51.78*
CRG 0332	CRG 0314	1.90*	-1.56	-0.61	12.40*	-135.91*	-11.74
CRG 0333	CRG 0312	-0.38	0.50	-2.04*	14.95*	301.42*	31.48*
CRG 0333	CRG 0314	1.60*	5.05*	-0.92*	12.17*	-6.80	-22.73*
CRG 0333	CRG 0332	-1.02*	10.79*	0.77	-1.10	-93.31	-56.41*
CRG 0347	CRG 0312	1.02*	-0.62	0.24	8.41*	148.74*	16.69*
CRG 0347	CRG 0314	0.22	3.29*	0.07	2.51	-284.57*	-42.70*
CRG 0347	CRG 0332	-0.41	3.11*	1.66*	-2.10	-120.15*	-37.66*
CRG 0347	CRG 0333	-0.27	0.14	0.82	-4.59*	-22.61	-1.82
CRG 0537	CRG 0312	-3.35*	-2.28*	2.80*	-7.21*	-193.40*	-19.37*
CRG 0537	CRG 0314	1.03*	1.35	3.57*	-8.80*	-408.16*	-45.99*
CRG 0537	CRG 0332	-1.01*	3.96*	4.17*	-17.48*	-261.19*	-51.61*
CRG 0537	CRG 0333	-1.64*	0.06	3.15*	-19.90*	-278.81*	-31.87*
CRG 0537	CRG 0347	-1.84*	-0.32	5.58*	-14.50*	-370.94*	-36.74*

†TCSA is the trunk cross-sectional area for juvenile(j) and reproductive(r) growth stages.

phase (P = 0.306), hundred bean weight (P = 0.115) and yield efficiency (P = 0.308). Generally, points above the regression line reflect gain from ortet selection for the particular trait, and *vice versa*. For TCSA during the pod-bearing phase, a much higher than expected increase in TCSA of scion CRG 0314 accounted for the lack of significance of the regression slope. Without CRG 0314, the r^2 value of 0.255 (P = 0.306) improves to r^2 = 0.756 (P = 0.02). Similarly, a much higher bean weight of the ortet selected from CRG 0333 accounted for loss of prediction. Omitting this clone's performance improves the r^2 = 0.501 (P = 0.115) to r^2 = 0.955 (P < 0.001). For yield efficiency, the low clonal value of CRG 0537 relative to its seedling family performance resulted in an improvement of the r^2 values from 0.254 (P = 0.308) to 0.728 (P = 0.031) when CRG 0537 was omitted from the regression analysis.

Discussion

For the genotypes tested, only CRG 0314 had high yield and yield efficiency performance as a full-sib family when used as a rootstock or scion in the clonal plantings. In previous trials (Adomako, 1999; CRIG, 2014), this genotype, CRG 0314, has shown exceptional performance at the juvenile and reproductive phases of growth. On the other hand, CRG 0332 showed that when the full-sib family has poor expression for yield and yield efficiency, its use as a rootstock leads to corresponding poor yields. This corroborates Murray and Cope (1959) findings that the yield of a high yielding clone cannot be increased by growing it on a rootstock that is itself no higher yielding than the scion. Similar observations were made in kiwi fruits (Cruz-Castillo et al., 1997) and avocado (Ben-Ya'acov et al., 1992) where productive trees from commercial and experimental plantations led to substantial yield improvement when these were used as rootstock. As extensive rooting plants are better at locating soil nutrients and water, and redistributing same to the upper layers for plant use (Bayala and Prieto, 2020); high yielding cocoa varieties with excellent rootstock potential may have developed better rooting architecture.

Generally, GC appears a reliable statistic to predict the performance of a full-sib family as a good rootstock or scion. In relation to the GC values, CRG 0314 was distinctive in its superiority for the measured traits, in agreement with its performance in the full-sib progeny. In conformity with its favourable GC values, CRG 0314 showed good performance both as a clone and as a scion for the measured traits, affirming the agronomic potential of this genotype. In contrast, CRG 0332 with its negative GC for the two vigour traits imparted the least vigour to clonal plants whether as rootstock or scion. In previous observations on cocoa (Padi et al., 2012), full-sib families that develop large trunk diameters early in their growth cycle generally had larger bean yields. Several other researchers have made similar observations for grafted fruit trees including pistachio (Crane and Iwakiri, 1986), peach (Yadava and Doud, 1989), kiwi fruit (Wang et al., 1994), apple (Hirst and Ferree, 1995) and kola (Akpertey et al., 2017). As rootstocks can influence tree growth and size of the vessel elements of the trunk of the scion (Vasconcellos and Castle, 1994) resulting in more vascular tissue for transport of water, minerals, carbohydrate reserves, and plant growth substances to the scion (from rapid increases in TCSA) would promote canopy development and early yields. In agreement with these observations, in the present study, the juvenile vigour performance (TCSAj) of full-sib families as rootstocks were predictive of their dry bean yield performance. For a particular scion, the least yields were realized on the least vigorous full-sib family, CRG 0332, used as rootstock.

In the present study, the lack of rootstock x scion interaction, and non-significance of SC component implies that once a good rootstock is obtained, it would impart good growth and yield to any good scion grafted onto it. This emphasizes the importance of additive gene action in the expression of the assessed traits over non-additive gene action. Through the diallel approach used in the present study, the reciprocal effect reveals a genotype's relative suitability either as a rootstock or scion. For both yield and yield efficiency, the negative reciprocal effects associated with CRG 0537 as rootstock, and significant positive estimates associated with CRG

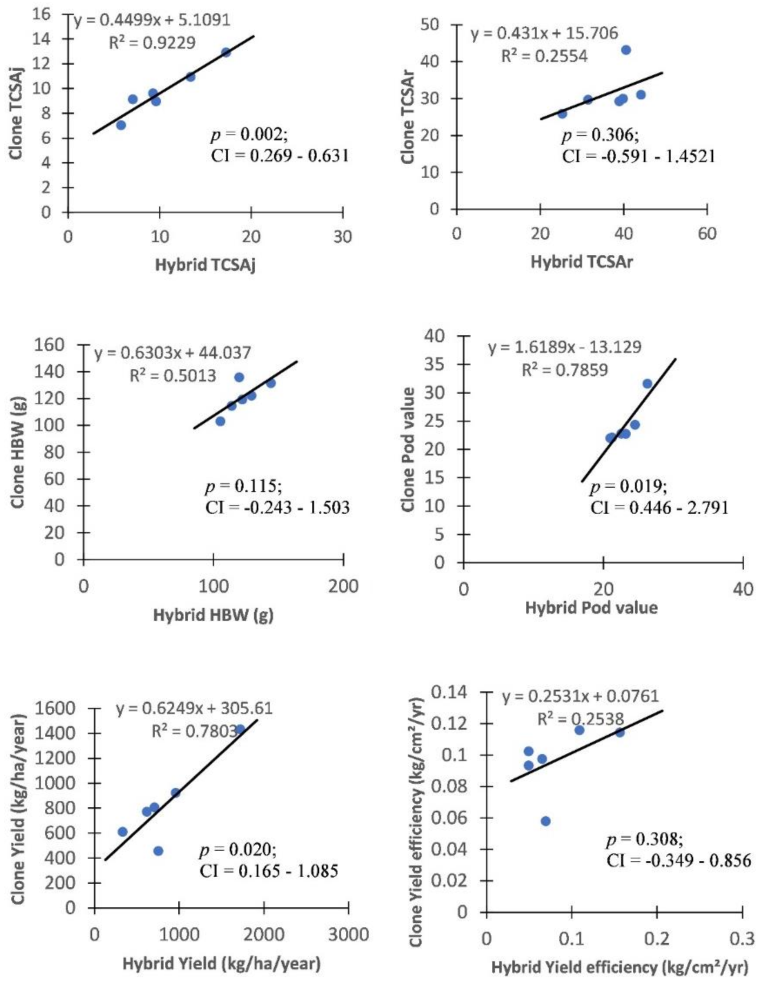

Fig 2. Slope characteristics from hybrid – clone regression of six cocoa genotypes evaluated in a field experiment over six years. Clones utilised data from only homografting; and hybrids from family performance.

0312 as scion reveal these as good rootstocks with general suitability for a good scion. In combination with the best scion genotypes namely, CRG 0314, 0332 and 0333, these rootstocks (CRG 0537 and CRG 0312) provide productive clonal varieties. A similar lack of rootstock x scion interaction was reported in experiments conducted in Indonesia (Van der Knaap, 1953) and Malaysia (Chong and Shepherd, 1986) using different types of rootstocks and scions. As a derived trait from a ratio of yield to TCSA, yield efficiency is not easily predicted by either trait expression alone. Moreover, because of the general positive genetic correlation between TCSA and bean yield in cacao (Mustiga et al., 2018; Padi et al., 2012), using low vigour rootstocks to increase yield efficiency appears a counter-intuitive approach. Implied from the observations of Padi et al., 2012; 2017a, the ideal rootstock/scion combination to induce high yield efficiency should display rapid increase in trunk diameter during the juvenile phase (large TCSAj), and considerable reduction in vegetative growth during the pod bearing phase (low TCSAr). In the present study, only CRG 0332 as scion and CRG 0333 as rootstock approaches this objective, leading to a high yield efficiency in clone CRG 0333/CRG 0332, even with relatively low yields. In commercial plantings, such clones would need to be planted at densities higher than the conventional recommendation. Where changes to planting density are not considered to exploit yield efficiency, the commercial objective of achieving high yield efficiency must be achieved through high bean yields rather than reduced tree vigour. In our current analyses, only scion CRG 0314 with its large bean yield achieved high yield efficiencies with large TCSA during the reproductive phase by compensating with large bean yields.

An interesting observation in the present study is the lack of significance of the slopes from the full-sib progeny – clone regression for TCSAr, hundred bean weight and yield efficiency. Selection of superior trees from full-sib families for clone development (ortet selection) is often influenced by non-additive genetic effects that lead to superior trait expression in the clonal phase (Yadav et al., 2023). The high performance for TCSAr in CRG 0314, and larger bean of CRG 0333 in the clonal phase relative to the full-sib family performance attests to the involvement of non-genetic effects in the expression of these traits for the selected ortets. In forest trees, reported values indicate genetic gains of up to 15% in stem diameter growth, achieved through plus-tree selection (Cornelius, 1994) largely on account of exploiting non-additive genetic effects (Berlin et al., 2019). As seen in the graphical plots for yield efficiency among full-sib progeny and scion effect of clones, significant rank change occurred for CRG 0332 due to an 85% increase in yield of its scion relative to the full-sib progeny while maintaining its relatively low TCSA.

Table 6. Growth and yield performance of 36 cocoa clones evaluated over a six-year period (2017 to 2023).

Clones	TCSAj (cm^2)	TCSAr (cm^2)	HBW (g)	Pod value	Yield (kg ha^{-1} $year^{-1}$)	YE (kg cm^{-2} $year^{-1}$)
CRG 0312/CRG 0314	13.43	28.8	117.73	21.15	1.55	0.19
CRG 0333/CRG 0332	9.32	18.3	137.49	22.22	0.86	0.18
CRG 0333/CRG 0314	10.11	27.55	116.91	21.94	1.29	0.17
CRG 0347/CRG 0332	9.73	21.63	127.03	22.08	0.93	0.17
CRG 0537/CRG 0332	10.83	24.26	134.24	18.93	1.05	0.17
CRG 0312/CRG 0332	9.59	21.68	130.35	21.89	0.85	0.16
CRG 0332/CRG 0314	9.49	29.54	117.78	22.25	1.20	0.15
CRG 0347/CRG 0314	10.12	30.56	115.51	22.64	1.26	0.15
CRG 0537/CRG 0314	11.02	33.43	120.85	22.58	1.34	0.14
CRG 0314/CRG 0332	13.29	26.42	142.59	20.10	0.93	0.13
CRG 0314/CRG 0333	13.32	37.65	141.24	20.77	1.28	0.13
CRG 0333/CRG 0333	9.62	29.73	135.87	22.78	0.93	0.12
CRG 0312/CRG 0333	10.07	33.38	135.2	21.66	1.06	0.12
CRG 0314/CRG 0314	12.93	43.18	119.39	22.02	1.43	0.11
CRG 0537/CRG 0312	15.13	35.83	115.62	22.26	0.96	0.11
CRG 0312/CRG 0347	11.13	29.23	120.95	24.38	0.83	0.11
CRG 0537/CRG 0333	10.86	31.94	136.11	21.53	0.94	0.11
CRG 0312/CRG 0312	10.95	31.06	114.59	22.82	0.77	0.10
CRG 0537/CRG 0347	11.03	35.31	124.47	23.43	1.01	0.10
CRG 0347/CRG 0333	10.16	28.16	131.77	21.62	0.81	0.10
CRG 0347/CRG 0347	9.15	30.00	122.28	24.36	0.81	0.10
CRG 0333/CRG 0347	9.63	28.43	122.58	23.13	0.76	0.10
CRG 0332/CRG 0332	7.06	25.93	131.55	22.11	0.61	0.09
CRG 0332/CRG 0347	8.92	27.85	122.83	24.13	0.69	0.09
CRG 0314/CRG 0312	14.94	36.55	110.77	24.78	0.68	0.07
CRG 0347/CRG 0312	9.09	30.47	104.12	23.89	0.53	0.07
CRG 0312/CRG 0537	8.43	31.28	101.20	27.40	0.57	0.07
CRG 0314/CRG 0347	10.56	37.14	120.53	22.92	0.69	0.07
CRG 0332/CRG 0537	8.82	32.19	99.29	27.99	0.52	0.06
CRG 0332/CRG 0333	7.29	39.88	135.30	23.73	0.67	0.06
CRG 0537/CRG 0537	8.98	29.26	103.13	31.64	0.46	0.06
CRG 0332/CRG 0312	10.34	38.94	114.88	22.89	0.62	0.06
CRG 0314/CRG 0537	13.07	36.14	103.25	30.10	0.52	0.05
CRG 0333/CRG 0312	10.82	32.37	105.29	24.96	0.46	0.05
CRG 0333/CRG 0537	7.57	32.06	96.31	28.30	0.39	0.04
CRG 0347/CRG 0537	7.36	34.67	95.46	33.95	0.27	0.03
Mean	10.39	31.13	120.12	23.76	0.85	0.11
SED (df = 105)	1.87**	4.35**	7.37**	1.56**	0.20**	0.03**

* $P < 0.01$; †TCSA is the trunk cross-sectional area for juvenile(j) and reproductive(r) growth stages; PV is pod value, HBW is hundred bean weight; and YE is yield efficiency.

Our analyses that compared the performance of heterograft and homograft clones did not reveal significant differences in the vigour and productivity traits considered in the present study. This further illustrates that in cocoa, it is worthwhile to invest in rootstock genotypes that promote the productivity of scions as genotype incompatibility is not a barrier for grafted plants. In earlier studies by Cope (1949), observations that rooted cuttings were found superior to grafted cocoa of the same genotype led to the assumption of incompatibility of graft union in heterografts as a possible cause of lower yields. Moreover, Masseret et al. (2005) observed that cocoa plants raised from somatic embryoids grew about 40% faster than grafted clones from the same genotype, implicating a weakness in bud grafted plants. Findings by Mooleedhar (1998) and Goenaga et al. (2015), however, of similar pod production capacity between heterografted and somatic embryo-derived rooted cuttings of the same cocoa genotypes concur with the implications of the current study that graft union in heterografting is not a limitation to the agronomic potential of grafted cocoa clones.

Materials and Methods

Plant material

Based on the performance of six full-sib families in previous trials (Padi et al., 2017a, b), ortets were selected from each of these cocoa families and used to develop scions for clonal propagation. Within families, ortets were selected as plus trees based on the number of pods after individual tree value adjustment following Padi et al. (2013). The families CRG 0312, CRG 0314, CRG 0332, CRG 0333, CRG 0347, and CRG 0537 were selected largely based on differences in vigour characteristics, precocity, and yield. Collectively referred to as genotype, the description of the six selections for the scion and corresponding full-sib family used as rootstock are described by parentage in Table 7.

Full-sib families from which ortets were selected were regenerated as rootstock types. These were generated by manual pollination in May 2016 from parental trees in a germplasm collection of the Cocoa Research Institute of Ghana (CRIG). Pods were harvested in November 2016 and seeds nursed in a gauze-house facility for six months before transplanting to the field. A reciprocal grafting

Table 7. Description of cocoa genetic resources used by parentage and genetic group.

Genotype	Parentage*	Definition of parentage
CRG 0312	PA 107 x MAN 15-2	PA 107 is a Parinari clone belonging to the Marañón genetic group. MAN 15-2 is a clone of mixed parentage, but mainly of Purus genetic group.
CRG 0314	Pound 10 x SCA 9	Pound 10 is a clone belonging to the Nanay genetic group. SCA 9 belongs to the Scavina/ Contamana genetic group.
CRG 0332	AMAZ 15-15 x AMAZ 3-2	Both belong to the Iquitos genetic group
CRG 0333	PA 150 x CRG 9006	PA 150 is a Parinari clone belonging to the Marañón genetic group. CRG 9006 has the parentage GU 144 C x MAN 15-2.
CRG 0347	T79/501 x GU 255 V	T79/501 is of a Nanay x Parinari origin. GU 255 V is a clone belonging to the Guiana genetic group.
CRG 0537	MAN 15-2 x SCA 6	SCA 6 originates from Peru and belongs to the Scavina/Contanama genetic group.

*Genetic assignments follow Motamayor et al., 2008 and Padi et al., 2015.

approach was used to generate the test materials where the same set of genotypes used as rootstocks also served as scions. At two months after transplanting the rootstocks, scions from the ortets were grafted in-situ (hereinafter referred to as clones) in all the possible combinations between the six genotypes, including homografting to obtain 36 rootstock/scion combinations.

Study site characteristics

The study site is located at Akim Tafo, Eastern Region, Ghana in the Square Mile of the Cocoa Research Institute of Ghana (CRIG, latitude 06 ∘ 13'N, longitude 0 ∘ 22'W) at an altitude of 210 m above sea level. The area falls within the Moist Semi-deciduous agroecological zone. During the period of data collection reported in the present study, total annual rainfall (in mm) was 1434, 1398, 1594, 1395, and 1782 for 2019, 2020, 2021, 2022 and 2023, respectively. The corresponding average relative humidity (at 09 hours / 15 hours GMT) were 80/66 %, 79/62 %, 79/63 %, 80/61 % and 84/74 %. The average annual temperature was 23 °C min and 32 °C max, for the duration of the trial. Meteorological data were obtained from a weather station 100 m from the trial site.

The soil at the experimental site is characterized as Ferric Lixisols as described in the World Reference Base for soil resources (FAO/ISRIC/ISSS, 1998). Soil chemical properties of the experimental site were determined from analyses of samples taken from depths of 0–30 cm. Soil samples were obtained from each of four replicates for each of the two trials, each sample representing subsamples taken randomly from the replicate areas. Samples were air-dried, crushed, and subjected to standard analytical procedures for determination of textural class, soil organic carbon, soil pH, total nitrogen, Bray available phosphorus, exchangeable potassium, calcium, and magnesium (Table 8).

Trial establishment and crop management

The design and management conditions of the two experiments described in the present study were described in Anokye et al. (2024). Briefly, the progeny (full-sib experiment) and clonal trial (grafted experiment) trials were planted in May 2017 within rows of plantain at a spacing of 3 m × 3 m to obtain 1111 plants per ha using a randomized complete block design of 20 trees per plot with four replications. Two perimeter guard rows were planted around the trial using a mixed stand of the six seed-derived varieties, at the same spacing used for the experimental area.

Crop measurements

Data presented in the current analysis were taken over four-year period, from 30 to 76 months after transplanting cocoa to the field. Stem diameter of each cocoa tree at 15 cm above the soil surface was measured with electronic callipers, at six-monthly intervals. Bean yield data were recorded on each of the 20 trees in a plot for both trials. Recorded pod traits were taken on individual plant basis as pods ripened, and comprised the total number of wholesome matured pods, and the number of matured pods damaged by pod rot. Pod damaged by pod rot (black pod symptoms typically caused by *Phytophthora spp.*) was separated into pods with useable beans and discarded pods due to rotten beans. Dry bean yield per hectare from each plot was estimated from total useable pod production (the sum of wholesome and useable black pods) divided by the pod value. The pod value, defined as the number of pods needed to obtain 1 kg of dry beans was determined as average values estimated twice a year on plot basis using 30 pods sampled from all trees per plot. Fresh beans obtained from the pods were fermented for six days before drying to a moisture content of 8 %. The bean size was estimated as the weight of one hundred dried beans. The trunk cross-sectional area of each cocoa tree was estimated from the tree stem diameter measurements. Yield efficiency was estimated as the cumulative dry bean yield per tree from 30 MAT to the conclusion of yield recording (at 76 MAT) divided by the average trunk cross-sectional area per tree during the yield recording period.

Data analysis

Except for the incidence of pod rot caused by *Phytophthora* spp. that was not analysed due to very low incidence (damage generally below 5%), all measured traits in the progeny trial were analysed using GenStat statistical software, version 12 (VSN International Ltd, Hemel Hempstead, UK). Data obtained from the progeny and clone trials were observed for normality using the plot of residuals, and a one-way ANOVA model was used to analyse for differences between the six progenies. For the clone trials, General Compatibility, GC; and Specific Compatibility, SC effects of rootstock and scion combinations were estimated by adopting the diallel mating design (Griffing RCBD method I, model B) using the Analysis of Genetic Designs in R (AGD-R) software version 3.0 (Rodríguez et al., 2015). The approach follows the procedures of General Combining Ability and Specific

Table 8. Soil physical and chemical characteristics of the experimental field used to evaluate cocoa hybrids and clones over a six-year period

Soil properties	Grafting experimental plot		Progeny experimental plot		*Critical levels
Soil Depth (cm)	0-15	15-30	0-15	15-30	
pH	6.75±0.24	6.49±0.28	7.31±0.31	7.18±0.29	5.6 - 7.2
Organic C (%)	0.94±0.10	0.66±0.12	0.99±0.29	0.76±0.30	3.50
Total N (%)	0.09±0.01	0.06±0.01	0.10±0.02	0.06±0.02	0.09 – 0.12
Avail. P (μg / g)	43.01±0.97	38.69±0.90	51.80±4.22	51.54±6.46	15 - 20
Exch. K (cmol kg^{-1})	0.32±0.02	0.30±0.02	0.38±0.04	0.32±0.06	0.25
Exch. Mg (cmol kg^{-1})	1.56±0.11	1.22±0.18	2.24±0.61	1.79±0.53	1.33
Sand (%)	71.74±0.96	70.74±0.50	74.57±1.76	75.24±2.31	N/A
Clay (%)	13.76±1.00	14.76±0.00	12.76±2.00	12.76±2.00	N/A
Silt (%)	14.50±0.50	14.50±0.50	12.67±0.67	12.00±1.16	N/A
Textural Class (USDA Standard)	Sandy Loam				

*Critical levels = levels of soil parameters required for cocoa cultivation (Ahenkorah et al., 1982).

Combining Ability analyses of breeding experiments, but the terms Female and Male parents, were replaced with Rootstock and Scion, respectively. In addition, a two-way ANOVA of rootstock × scion was done to determine the performance of the six genotypes used in the trial. Differences between the 36 clones (rootstock – scion combinations) were analysed using a one-way ANOVA for the measured traits.

Significance of the slope of hybrid (progeny families) – clone plots were used to determine the predictability of the progeny family performance on that of their progenitor clones.

Conclusion

Three key observations may be summarized from the results of the present study.

First, with the rootstock x scion interaction variance not significant, and the specific compatibility component of the diallel analysis also not significant for any of the traits studied, a good rootstock would be broadly useful for any scion genotype to develop clonal cocoa varieties. This observation is strengthened by the parity in performance between homograft and heterograft clones. The full-sib families identified in the present study as good rootstocks should therefore be suitable to develop clonal varieties with any productive scion.

Second, though the effects of rootstock genotype on yield and yield efficiency cannot be discounted (largely through impact on TCSA on yield), rootstock effects were generally more significant for vegetative traits, whereas scion effects were more important for yield related traits. In general, the agronomic performance of full-sib cocoa families is a reliable predictor of its clonal counterpart. Full-sib families with high juvenile vigour proved more suitable as rootstock types, whereas the highest yields of clonal plants were predictable based on the yield of the full-sib family used as the scion. Therefore, the practical implication is that selecting full-sib family with good juvenile vigour as rootstock provides a good probability of realizing the yield potential of the scion genotype. As a logical corollary, use of half-sib progeny as rootstock should be avoided as such progeny are likely to segregate for vigour.

Overall, both yield and yield efficiency were similar in magnitude across the full-sib families and the clones. Rank changes in the yield efficiency between full-sib progeny and their clonal counterparts were evident for the materials used in this study. This was occasioned by CRG 0322, the genotype with the least vigour (estimated as TCSA) that had low yields in the full-sib family but increased significantly in bean yield from the scion developed through ortet selection. The scion genotype with the highest yield efficiency, CRG 0314, induced high TCSA with concurrent high bean yields. Yield efficiency in clonally propagated cocoa therefore may be achieved through grafting scions with high bean yield potential on rootstocks with low vigour such as CRG 0333/CRG 0332 or using vigorous rootstock and scion genotype of high bean yield to express high yield efficiency. Taking advantage of low-vigour clones with high yield efficiency in commercial plantings would require changes to planting density to maximize plants per unit area.

Acknowledgments

We acknowledge the support of the technical staff at the Physiology/Biochemistry Division of the Cocoa Research Institute of Ghana (CRIG). The Ghana Cocoa Board financed this work, and the article is published with the kind permission of the Executive Director, CRIG as manuscript number CRIG/01/2024/055/003.

Conflict of interest

The authors declare no conflict of interest.

Statement of contributions

Conceptualization: EA and FKP; methodology: EA and FKP, formal analysis: EA and FKP, data curation: EA; funding acquisition: EA; investigation: EA and FKP, supervision: EA and FKP; validation: EA and FKP; visualization: EA and FKP; project administration: EA; writing—original draft: EA and FKP; writing—review & editing: ED, SYO and FKP

References

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

Adu-Ampomah Y, Frimpong EB, Adomako B, Abdul-Karimu A (2005) Investigation into the use of the crinkled leaf mutant as a low vigour rootstock for high density planting in cocoa. Paper presented at the

International Workshop on Cocoa Breeding for Improved Production Systems, Accra, Ghana, 19-21 October 2003 (pp145-149).
Ahenkorah Y, Halm BJ, Appiah MR, Akrofi GS (1982) Fertilizer use on cacao rehabilitation projects in Ghana. Paper presented at the 8th International Cocoa Research Conference, Cartagena, Colombia, 1981(pp. 165-170).
Akpertey A, Dadzie AM, Adu-Gyamfi PKK, Ofori A, Padi FK (2017) Effectiveness of juvenile traits as selection criteria for yield efficiency in kola. Sci Hortic. 216:264–271.
Anokye E, Obeng-Bio E, Akpertey A, Aidoo MK, Aduama-Larbi MS, Padi FK (2024) Rootstock influences on growth and bearing precocity in juvenile cocoa. Ecol Genet Genom. 31: 100254.
Apshara E (2017) Comparative study on clonal and seedling progenies of selected cocoa (*Theobroma cacao* L.) genotypes. Indian J Hortic. 74: 168–172.
Armengot L, Picucci M, Milz J, Hansen JK, Schneider M (2023) Locally-selected cacao clones for improved yield: a case study in different production systems in a long-term trial. Front. Sustain. Food Syst. 7: 1253063.
Barden J, Cline J, Kushad MM, Parker ML (2002) Various measures of tree vigor, yield, and yield efficiency of apple trees in the 1990 NC-140 systems trial as influenced by location, cultivar, and orchard system. J Am Pomol Soc. 56: 208-214.
Bayala J, Prieto I (2020) Water acquisition, sharing and redistribution by roots: applications to agroforestry systems. Plant Soil. 453: 17–28.
Ben-Ya'acov A, Michelson E, Zilberstaine M, Barkan Z, Sela I (1992) Selection of clonal avocado rootstocks in Israel for high productivity under different soil conditions. Paper presented at the 2nd World Avocado Congress. Orange, Cal., USA (pp. 521-526).
Berlin M, Jansson G, Högberg KA, Helmersson A (2019) Analysis of non-additive genetic effects in Norway spruce. Tree Genet Genomes. 15: 42 10.1007/s11295-019-1350-9
Bloomberg (2024) Bloomberg website, https://www.bloomberg.com/news/articles/2024-03-25/cocoa-tops-9-000-as-supply-fears-keep-sparking-fresh-records Accessed: 25th March, 2024.
Chong CF, Shepherd R (1986) Promising Prang Besar clones. In: Cocoa and Coconuts: Progress and Outlook, 3–20. (Eds: E. Pushparajah and Chew Poh Soon). Kuala Lumpur: Incorporated Society of Planters.
Cohen S, Naor A (2002) The effects of three rootstocks on water use, canopy conductance and hydraulic parameters of apple trees, and predicting canopy from hydraulic conductance. Plant Cell Environ. 25: 17–28.
Cope FW (1949) Some results of the cacao clonal trials at River Estate, Trinidad. Report of the Cocoa Conference, Grosvenor House, London, 30 July – 1 August, 1949, The Cocoa, Chocolate and Confectionary Alliance Limited, 86-88.
Cornelius J, (1994) The effectiveness of plus-tree selection for yield. Forest Ecol Manag. 67(1-3):23-34.
Crane JC, Iwakiri BT (1986) Pistachio yield and quality as affected by rootstock. HortScience. 21: 1139 – 1140.
CRIG (2014) Annual report. Cocoa Research Institute of Ghana 2013/2014. CRIG Akim Tafo, Ghana Cacao Board, 217 p. https://www.crig.org.gh/articles-publications
Cruz-Castillo JG, Lawes GS, Woolley DJ, Ganesh S (1997) Evaluation of rootstock and 'Hayward' scion effects on field performance of kiwifruit vines using a multivariate analysis technique, New Zeal J Crop Hort. 25: 273-282.
Daymond AJ, Hadley P, Machado RCR, Ng E (2002) Genetic variability in the partitioning to the yield component of cacao (*Theobroma Cacao* L.). HortScience. 37(5): 799- 801.
Efron Y, Tade E, Epaina P (2003a) A cocoa growth mutant with a dwarfing effect as rootstock. Paper presented at the International Workshop on Cocoa Breeding for Improved Production Systems, Accra, Ghana, October 19–21, 2003 (pp. 132-21).
Efron Y, Epaina P, Tade E, Marfu J (2003b) The relationship between vigour, yield and yield efficiency of cocoa clones planted at different densities. Paper presented at the International Workshop on Cocoa Breeding for Improved Production Systems, Accra, Ghana, October 19–21, 2003 (pp. 92-102).
FAO/ISRIC/ISSS (1998) World Reference Base for Soil Resources. World Soil Resources Report, #84. FAO, Rome, 88pp.
Glendinning DR (1967) Technical aspects of the breeding programme at the Cocoa Research Institute, Tafo, Ghana. I. Breeding Methods. Euphytica. 16: 76–82.
Goenaga R, Guiltinan M, Maximova S, Seguine E, Irizarry H (2015) Yield performance and bean quality traits of cacao propagated by grafting and somatic embryo-derived cuttings. HortScience. 50: 358-362.
Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci. 9: 463-493.
Herklots GAC, Murray DB (2005) Cacao yields from clones and seedlings/ comparison of seedlings and cuttings as planting material. INGENIC Newslett. 10: 30-32.
Hirst PM, Ferree DC (1995) Rootstock effects on shoot morphology and spur quality of 'Delicious' apple and relationships with precocity and productivity. J Am Soc Hortic Sci. 120(4): 622-634.
ICCO 2024 Cocoa Market Review April 2024. International Cocoa Organization. Accessed online https://www.icco.org/wp-content/uploads/Cocoa-Market-Report-April-2024.pdf.
Irizarry H, Goenaga R (2000) Clonal selection in cacao based on early yield performance of grafted trees. J Agr U Puerto Rico. 84: 153–163.
Lachenaud PH (1995) Variations in the number of beans per pod in *Theobroma cacao* L. in the Ivory Coast. II. Pollen germination, pod loading and ovule development. J Hort Sci. 70: 1–6.
Lachenaud PH, Paulin D, Ducamp M, Thevenin JM (2007) Twenty years of agronomic evaluation of wild cocoa trees (*Theobroma cacao* L) from French Guiana. Sci Hortic. 113(4): 313–321.
Larsen FE, Higgins SS, Dolph CA (1992) Rootstock influence over 25 years on yield, yield efficiency and tree growth of cultivars 'delicious' and 'Golden delicious' apple (*Malus domestica* Borkh.). Sci Hortic. 49: 63–70.

Manu M, Tetteh EK (1987) A guide to cocoa cultivation. Cocoa Research Institute of Ghana (CRIG), 51 pages.

Masseret B, Alvarez M, Fontanel A, Pétiard V. (2005) Conformity of cocoa trees produced via somatic embryogenesis. Paper presented at the Malaysian International Cocoa Conference, 18-19 July, 2005 (pp. 122-130).

Mooleedhar V. (1998) A review of vegetative propagation methods in cocoa in Trinidad and the implications for mass production of clonal cocoa plants. Paper presented at the 'Technical Meeting': State of knowledge on mass production of genetically improved propagules of cocoa, October 19th to 23rd 1998 Oct (pp. 122-125).

Motamayor JC, Lachenaud P, Da Silva e Mota JW, Loor R, Kuhn DN, Brown JS, Schnell RJ (2008) Geographic and genetic population differentiation of the Amazonian chocolate tree (Theobroma cacao L). PloS ONE. 3(10):e3311.https://doi.org/10.1371/journal.pone.0003311.

Murray DB, Cope FW (1959) A stock-scion experiment with cacao III. Report on Cacao Research 1957-58, Imperial College of Tropical Agriculture, Trinidad, 29-35.

Mustiga GM, Gezan SA, Phillips-Mora W, Arciniegas-Leal A, Mata-Quirós A, Motamayor JC (2018) Phenotypic description of Theobroma cacao L. for yield and vigor traits from 34 hybrid families in Costa Rica based on the genetic basis of the parental population. Front Plant Sci. 9: 808. https://doi.org/10.3389/fpls.2018.00808.

Ofori A, Padi FK, Akpertey A, Adu-Gyamfi P, Dadzie MA, Amoah FM (2017) Variability of survival and yield traits in cacao (*Theobroma cacao* L.) clones under marginal field conditions in Ghana. J Crop Improv. 31(6):847-61.

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, Takrama J, Opoku SY, Dadzie AM, Assuah M (2013) Early stage performance of cocoa clones in relation to their progenitor ortets: implications for large-scale clone selection. J. Crop Improv. 27: 319–341.

Padi FK, Ofori A, Takrama J, Djan E, Opoku SY, Dadzie AM, Bhattacharjee R, Motamayor JC (2015) The impact of SNP fingerprinting and parentage analysis on the effectiveness of variety recommendations in cacao. Tree Genet Genomes. 11:1-4. https://doi.org/10.1007/s11295-015-0875-9.

Padi FK, Ofori A, Arthur A (2017a) Genetic variation and combining abilities for vigour and yield in a recurrent selection programme for cacao. J Agric Sci. 155 (3):444-64.

Padi FK, Ofori A, Akpertey A (2017b) Genetic base-broadening of cacao for precocity and cropping efficiency. Plant Genet Resour-C. 15(6):548–57. doi:10.1017/S1479262116000277.

Posnette AF (1951) Progeny trials with cocoa in the Gold Coast. Empire J Exp Agri. 19:242–252.

Reddy YT, Kurian RM, Ramachander PR, Singh G, Kohli RR (2003) Long-term effects of rootstocks on growth and fruit yielding patterns of 'Alphonso'mango (*Mangifera indica* L.). Sci Hortic. 97(2):95-108.

Rodríguez F, Alvarado G, Pacheco Á, Crossa J, Burgueño J (2015) AGD-R (Analysis of genetic designs with R for Windows) version 4.0. International Maize and Wheat Improvement Center (CIMMYT).

Sounigo O, N'Goran J, Paulin D, Clément D, Eskes AB (2005) Individual tree variation and selection for yield and vigour: Experience from Côte d'Ivoire. Paper presented at the International Workshop on Cocoa Breeding for Improved Production Systems pp. 66-73.

Susilo AW, Sulastri D, Djatiwaloejo S (2005) Selection and estimation the genetic parameters of rootstock characteristics on cocoa seedling of half-sibs families. Pelita Perkebunan. 21(3):147-158.

Tabe-Ojong MP, Guedegbe OTA, and Joseph Glauber J (2024) Soaring cocoa prices: Diverse impacts and implications for key West African producers. IFPRI Blog International Food Policy Research Institute. Accessed online https://www.ifpri.org/blog/soaring-cocoa-prices-diverse-impacts-and-implications-key-west-african-producers/ Accessed: August 31, 2024.

Thomas E (2024) Cocoa prices continue to rise. When might the tide turn? JustFood Global Food Industry News, Market Research and Reports. Accessed online: https://www.just-food.com/features/cocoa-prices-continue-to-rise-when-might-the-tide-turn/?cf-view Accessed April 10, 2024.

Tombesi S, Almehdi A, DeJong TM (2011) Phenotyping vigour control capacity of new peach rootstocks by xylem vessel analysis. Sci Hortic. 127 (3): 353–357.

Van der Knaap WP (1953) General considerations regarding the factors that affect the productive capacity of cocoa clones. Archief voor de Koffiecultuur. 17:121-40.

Van Hall CJJ (1932) Cacao. 514 pages. 2nd edition (London: Macmillan and Co., Ltd., 1932).

Vasconcellos LA, Castle WS (1994) Trunk xylem anatomy of mature healthy and blighted grapefruit trees on several rootstocks. J Am Soc Hortic Sci. 19(2):185-194.

Wang ZY, Patterson KJ, Gould KS, Lowe RG (1994) Rootstock effects on budburst and flowering in kiwifruit. Sci Hortic. 57(3):187-199.

Yadav S, Ross EM, Wei X, Powell O, Hivert V, Hickey LT, Atkin F, Deomano E, Aitken KS, Voss-Fels KP, Hayes BJ (2023) Optimising clonal performance in sugarcane: leveraging non-additive effects via mate-allocation strategies. Front Plant Sci. 10: 14:1260517. doi: 10.3389/fpls.2023.1260517.

Yadava UL, Doud SL (1989) Rootstock and scion influence growth, productivity, survival, and short life-related performance of peach trees. J Amer Soc Hort Sci. 114:875-880.

Yin JP (2004) Rootstock effects on cocoa in Sabah, Malaysia. Exp Agr. 40(4):445-52.
https://doi.org/10.1017/S0014479704002108.