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PATH ANALYSIS OF YIELD COMPONENTS OF CACAO HYBRIDS (*Theobroma cacao* L.)*

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ABSTRACT

Genotypic correlations and their direct and indirect effects were estimated for ten traits of 12 cacao hybrids using path analysis. A high coefficient of genotypic correlation was found between trunk height and bean dry weight/tree. However, path analysis revealed that trunk height had a negative direct effect on yield. The number of healthy fruits/tree and dry bean weight/fruit should be considered as the main yield components because these traits showed direct effects of high value on dry bean weight/tree. The number of seeds/fruit and bean dry weight constituted the main components of dry bean weight/fruit. Since these traits showed direct and indirect effects of high value, they should be considered as secondary yield components.

INTRODUCTION

In improvement studies carried out at research centers working with cacao (*Theobroma cacao* L.), special emphasis has been placed on the maximization of yield in new plantations. Productivity, like most traits of economic importance, is of complex inheritance and may involve several characters. This means that selection for a given trait can provoke a simultaneous change in one or more other traits (Robinson *et al.*, 1951) with the consequent need to learn about the degree of association between such traits. However, correlation estimates do not provide an exact view of the direct and indirect effects of each primary component on productivity (Bhatt, 1973).

For a more appropriate understanding of the causes of association between traits, Wright (1921, 1934) proposed path-coefficient analysis which permits the partition of correlations coefficients into direct and indirect effects since the correlation between two variables is the result of the sum of the values for all effects associated with the two variables (Li, 1977).

This method, which is considered to be a generalization of standardized partial regression analysis, consists of the study of a system of multiple, linearly related variables involving the basic factors (causes) and their resulting variables (effects) (Li, 1977).

The path-coefficient method has proved to be a valuable tool for revealing the true nature of cause-effect interrelations between yield and its primary components. Many studies have been published on the use of path-coefficient analysis for various plant species of economic importance such as rice (Morais, 1980), sweet potatoes (Miranda *et al.*, 1988), guaraná (Nascimento Filho, 1988), maize (Viana *et al.*, 1980), peppers (Cruz *et al.*, 1988), rubber trees (Paiva *et al.*, 1982; Vasconcelos, 1982) and wheat (Bhatt, 1973; Ehdaie and Waines, 1989).

The objective of the present study was to evaluate the genotypic correlations and their partitions into direct and indirect effects by path analysis of some yield components of cacao.

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MATERIAL AND METHODS

The study was conducted at the "Paulo Dias Morelli" Experimental Station-ESPAM (3°30'30" S, 52°58'30" W), headquarters of CEPLAC, located at km 100 on the Trans-Amazon highway in the Altamira-Itaituba direction, municipality of Medicilândia, PA. Two trials were set up in contiguous areas to determine the behavior of 38 cacao hybrids under the environmental conditions of Altamira, PA.

Among the established genetic materials available, 12 hybrids were selected for the trial. Six were assigned to experiment D-1, four to experiment D-2 and two (IMC 67 x CATONGO and SCA 6 x ICS 1) were assigned to both experiments. The following materials were used:

Experiment D-1		Experiment D-2	
1. IMC 67	x CA 4	7. POUND 12	x SIAL 505
2. POUND 7	x SIAL 505	8. POUND 12	x SIC 329
3. POUND 7	x BE 10	9. PA 121	x SIC 329
4. POUND 12	x BE 10	10. PA 150	x BE 10
5. PA 150	x SIC 328	A. IMC 67	x CATONGO
6. SCA 6	x BE 10	B. SCA 6	x ICS 1
A. IMC 67	x CATONGO		
B. SCA 6	x ICS 1		

The trials were set up in May 1978 using the following technical guidelines: a) spacing of cacao trees: 3.0 x 3.0 m, and b) spacing of definitive shading: 24.0 x 24.0 m, with a tree in the diagonal. *Erythrina poeppigiana* (erythrina) was used for definitive shading in experiment D-1, and *Plathymenia foliolosa* ("vinhático") for experiment D-2.

Both trials were designed as randomized blocks with seven replications and 12 plants per plot.

The following traits were tested: a) bean dry weight/tree (BDWT), kg/tree; b) trunk height (TH), cm; c) trunk diameter (TD), cm; d) number of healthy fruits/tree (NHFT); e) number of beans/fruit (NBF); f) individual bean dry weight (IBDW), g) bean dry weight/fruit (BDWF), g/fruit; h) fruit weight (FW), g; i) fruit index (FI) or number of fruit needed to make up 1 kg dry cacao; j) rate of bean moist weight conversion to bean dry matter (RC), as a percentage.

The following procedures were used to estimate BDWT, IBDW, BDWF, FI, and RC: a) BDWT: [bean moist weight/tree (BMWT).RC]/100; b) IBDW: bean dry weight/number of sampled beans (usually 50); c) BDWF: [bean moist weight/fruit (BMWF).RC]/100; d) FI: 1000/BDWF; e) RC: (100. bean dry weight)/bean moist weight (usually 50).

Traits TH and TD were obtained in 1986 and 1987, respectively; NHFT, BMWT and BMWF were obtained in 1987 during biweekly programmed collections. The remaining variables were obtained in 1987 by fruit sampling from tree to tree, for a minimum of two and a maximum of five fruits at two different times of year as follows: a) May/June - period during which the collected fruits had developed under conditions of excess water, and b) September/October - period during which the collected fruits had developed under conditions of water deficiency.

The values obtained for FW, NBF, IBDW, FI and RC represent the mean of the two above periods, whereas those obtained for BDWF and BDWT represent the annual mean of the generating variables.

More detailed experimental data have been published by Almeida (1991).

Genotypic correlations (r_G) were estimated by the method of Mode and Robinson (1959) and later partitioned into direct and indirect effects by path analysis (Li, 1977).

Three hypothesis were considered for path analysis: a) BDWT as dependent variable and TH, TD, NHFT, NBF, IBDW, BDWF, FW, FI and RC as explicative variables; b) BDWT as dependent variable and NHFT, NBF, IBDW and BDWT as explicative variables according to Soria (1977, 1978), and c) BDWF as dependent variable and FW, NBF, IBDW and RC as explicative variables.

RESULTS AND DISCUSSION

The estimated r_G coefficients between the traits analyzed are presented in Table I, and their partitioning into direct and indirect effects is presented in Tables II, III and IV.

Table II contains the partitioning of the r_G coefficients for TH, TD, NHFT, NBF, IBDW, BDWF, FW, FI and RC over BDWT.

It can be seen that BDWT presented the highest degree of genotypic association with TH, followed by NHFT (Table I). However, the direct genotypic effect of TH was negative and of low value (Table II), demonstrating that this variable does not represent, by itself, a relevant yield component. This means that the indirect effects represent the cause of correlation and, in this case, the positive indirect effect via NHFT is largely responsible for the high r_G value obtained. Since the height of the cacao tree trunk is maximum at approximately 12 to 18 months of age after planting in the field (Charrier, 1969), it is concluded that this variable should also be devoid of indicative value for indirect selection during the early planting phase. The little influence of TH on BDWT may be similarly visualized through its indirect effects in relation to the remaining traits, which were always of low magnitude. This fact suggests that selection on the basis of

Table I - Genotypic correlation coefficients estimated between ten traits of adult hybrid cacao trees.

Traits	TH	TD	NHFT	NBF	IBDW	BDWF	FW	FI	RC[a]
Bean dry weight/tree (BDWT)	0.958	0.153	0.836	0.099	-0.030	-0.017	-0.480	-0.055	-0.302
Trunk height (TH)		0.034	0.882	-0.172	0.020	-0.204	-0.697	0.120	-0.448
Trunk diameter (TD)			-0.135	0.084	0.263	0.454	0.219	-0.263	-0.294
Number of healthy fruits/tree (NHFT)				-0.267	-0.446	-0.563	-0.822	0.486	-0.502
Number of beans/fruit (NBF)					0.081	0.671	0.466	-0.756	0.778
Individual bean dry weight (IBDW)						0.730	0.644	-0.702	0.224
Bean dry weight/fruit (BDWF)							0.778	-0.967	0.441
Fruit weight (FW)								-0.733	0.499
Fruit index (FI)									-0.716

[a]RC, Rate of conversion.

Table II - Path analysis: partitioning of genotypic correlations into direct (on the diagonal) and indirect (outside the diagonal) effect components of nine agronomic traits on bean dry weight/tree (BDWT) for adult hybrid cacao trees.[a]

Traits	TH	TD	NHFT	NBF	IBDW	BDWF	FW	FI	RC	Total[b]
Trunk height (TH)	-0.077	0.002	1.085	-0.015	0.003	0.106	0.072	0.0005	-0.007	0.958
Trunk diameter (TD)	-0.002	0.059	-0.166	0.007	0.048	0.235	-0.022	-0.001	-0.005	0.153
Number of healthy fruits/tree (NHFT)	-0.068	-0.008	1.230	-0.023	-0.083	-0.291	0.085	0.002	-0.008	0.836
Number of beans/fruit (NBF)	0.013	0.005	-0.329	0.086	0.015	0.347	-0.048	-0.003	0.013	0.099
Individual bean dry weight (IBDW)	-0.001	0.015	-0.548	0.007	0.185	0.378	-0.067	-0.003	0.004	-0.030
Bean dry weight/fruit (BDWF)	0.016	0.027	-0.693	0.058	0.135	0.517	-0.080	-0.004	0.007	-0.017
Fruit weight (FW)	0.054	0.013	-1.011	0.040	0.119	0.403	-0.103	-0.003	0.008	-0.480
Fruit index (FI)	-0.009	-0.016	0.597	-0.065	-0.130	-0.500	0.076	0.004	-0.012	-0.055
Rate of conversion (RC)	0.035	-0.017	-0.618	0.067	0.041	0.228	-0.052	-0.003	0.017	-0.302

[a]Indirect effects are read horizontally.
[b]Coefficients of genotypic correlation with bean dry weight/tree (BDWT).

Table III - Path analysis: partitioning of genotypic correlations into direct (on the diagonal) and indirect (outside the diagonal) effect components of four agronomic traits on bean dry weight/tree (BDWT), referring to adult hybrid cacao trees.[a]

Traits	NHFT	NBF	IBDW	BDWF	Total[b]
Number of healthy fruits/tree (NHFT)	1.214	0.003	-0.019	-0.362	0.836
Number of beans/fruit (NBF)	-0.324	-0.011	0.003	0.431	0.099
Individual bean dry weight (IBDW)	-0.541	-0.001	0.042	0.470	-0.030
Bean dry weight/fruit (BDWF)	-0.683	-0.007	0.030	0.643	-0.017

[a]Indirect effects are read horizontally.
[b]Coefficients of genotypic correlation with bean dry weight/tree (BDWT).

Table IV - Path analysis: partitioning of genotypic correlations into direct (on the diagonal) and indirect (outside the diagonal) effect components of four agronomic traits on bean dry weight/fruit (BDWF), referring to adult hybrid cacao trees.[a]

Traits	FW	NBF	IBDW	RC	Total[b]
Fruit weight (FW)	0.178	0.443	0.424	-0.267	0.778
Number of beans/fruit (NBF)	0.083	0.951	0.053	-0.416	0.671
Individual dry bean weight (IBDW)	0.114	0.077	0.658	-0.120	0.730
Rate of Conversion (RC)	0.089	0.740	0.147	-0.535	0.441

[a]Indirect effects are read horizontally.
[b]Coefficients of genotypic correlation with bean dry weight/fruit (BDWF).

TH should not produce any changes in the remaining variables studied. This feature may be useful for programs of selection of genotypes resistant to witches' - broom [*Crinipellis perniciosa* (Stahel) Singer], the major disease attacking cacao trees in the Brazilian Amazon Region, since control of this disease is much easier in shorter trees.

NHFT had the highest direct effect on BDWT, indicating that this trait is the major yield component since the r_G coefficient was high (Table II) and all of its positive or negative indirect effects through the remaining explicative variables were of very low or relatively low values. These indirect effects partially explain the high genotypic correlation between BDWT and NHFT. In view of the fact that genotypic correlation explains the true association, we infer that direct selection through NHFT can be used to maximize selection for yield.

BDWF was the second component with the highest direct effect (Table II) on BDWT. However the r_G coefficient was of very low and negative value, indicating that the indirect effects are the cause of the lack of correlation, with emphasis on the indirect effect via NHFT which was of high and negative value.

The direct effect of TD on BDWT (Table II) was positive but of very low magnitude to be of any practical value in improvement programs. Its indirect effects in relation to the remaining variables were also of low magnitude. The indirect effect via NHFT reflected in almost all of its magnitude the values of the genotypic correlation between TD and NHFT.

NBF had a low direct effect (Table II) which, however, was quite similar to the r_G coefficient, demonstrating that the genotypic correlation expressed the true association. The opposite influences between indirect effects, especially between NHFT and BDWT reflect the result observed.

With respect to IDWT (Table II), the direct effect was of low value; the indirect effects via BDWF and NHFT markedly contributed to the fact that the r_G coefficient did not express the magnitude of the direct effect of this trait.

A similar situation was also observed for the r_G coefficients of FW, FI and RC, whose opposite influences exerted through the indirect effects between NHFT and BDWF were the major factors responsible for the sign and for the expression of the magnitudes of these coefficients. FW, FI and RC also had direct effects of low value on BDWT.

The low magnitudes of the direct and indirect effects of FI, RC, TD, TH and FW when compared to the remaining traits suggest that these variables seem to be of little importance in selection programs aiming at the maximization of yield (Table II).

The degree of genotypic determination [$R^2(2, 3, ... 10)$] was equal to 1.0, revealing that the residual component was reduced to zero. Thus, the explicative variables considered genotypically explained 100% of BDWT through their direct and indirect effects.

Table III presents the partitioning of the r_G coefficients for NHFT, NBF, IBDW and BDWF over BDWT. These variables are considered by Soria (1977, 1978) to be the major yield components.

Path analysis revealed that BDWT was mainly a consequence of NHFT and BDWF (Table III). The highest direct effect was that of NHFT, in agreement with the high r_G coefficient between these variables.

BDWF also had a relevant direct effect on BDWT (Table III). However, the correlation between these traits was negligible, not reflecting the true direct association. The sizable negative indirect effect via NHFT neutralized the direct effect of BDWF on BDWT, explaining the low value of the r_G coefficient obtained.

The low direct effects of NBF and IBWF are relatively compatible with the low values of their respective correlation coefficients (Table III). The indirect effects of NHFT and BDWF, of approximately similar values although of different signs, explain the values observed.

The extremely low values of the direct effects of NBF and IBDW indicate programs that these variables should not be considered in genetic improvement programs aiming at direct maximization of yield. In contrast, NHFT and BDWF were shown to be primary yield components, in agreement with studies conducted by Jacob and Toxopeus (1971), Atanda (1972), Jacob and Atanda (1973) and Atanda and Jacob (1975). However, it should be pointed out that in each correlation involving explicative variables and BDWT (Tables II and III), there was always a simultaneity of effects of considerable magnitudes but of different signs for NHFT and BDWF. This fact seems to support the biological argument of internal competiton for photosynthates within the tree (Alvim, 1977; Hutcheon, 1977) as more fruits are produced. This factor should serve as a warning to breeders since it represents a complicating element in selection when opting for the simultaneous inclusion of NHFT and BDWF as predictors of the yield potential of cacao genetic materials. Increased fruit production per tree in most cases will imply reduction of BDWT, and attaining additional genetic gains in yield *per se* will depend on the adoption of some strategies to circumvent the manifestation of the opposite forces exerted by NHFT and BDWT: a) identification of genetic materials which simultaneously express elevated magnitudes for NHFT and BDWT, and b) identification of genetic materials less sensitive to seasonal factors and of high productive ability, but presenting fruit production better distributed throughout the year.

In physiological terms, elevated NHFT and BDWF values reflect a better division of assimilated substances in the tree for economic yield.

Similarly to the result obtained by the path analysis described earlier, the degree of genotypic determination of BDWT through the four explicative variables considered (NHFT, NBF, IBDW and BDWF) also reached the maximum values, R^2 (2, 3, 4 and 5) = 1.0. Thus, we may conclude that 100% of the BDWT variation was genotypically explained by these variables.

The agreement of the results obtained using the two analysis described seems to reside in the fact that the explicative variables considered also included the primary yield components.

The fruit traits which must effect BDWF are grouped in Table IV. Thus, we partitioned the r_G coefficients of FW, NBF, IBDW and RC over BDWF.

It can be seen that NBF had the highest direct effect on BDWF (Table IV), in agreement with the r_G coefficient of 0.671 between these two variables. The direct effect of IBDW was also of high magnitude and relatively similar to the r_G coefficient, indicating that genotypic correlation is a reliable element for expressing the legitimate interrelation of this variable with BDWF.

FW had a low effect, which was incompatible with the high correlation (Table IV). In this case, the indirect effects represented the cause of genotypic correlation, especially through NBF and IBDW.

A high negative effect was observed for RC (Table IV), in contrast to the value observed for the r_G coefficient. The direct effect mainly exerted be NBF and IBDW, explains the estimates obtained.

In synthesis, path analysis involving fruit-related variables permitted the identification of NBF and of IBDW as the major factors responsible for BDWF. Thus, these traits should be considered as secondary yield components.

The relative importance detected for IBDW will also permit satisfying the requirements of the chocolate industry in terms of maintaining this variable at a weight of approximately one gram.

According to the estimate of the determination coefficient [R^2(2, 3, 4, and 5) = 1.0], the explicative variables considered (FW, NBF, IBDW and RC) involved 100% of the variation in BDWF, rendering the residual component null.

The above considerations demonstrate the importance of partitioning the correlations on the basis of direct and indirect effects, thus providing a more consistent interpretation of the results obtained, especially when the genotypic correlations do not reflect the true association between the variables considered. Simple correlation only quantifies the mutual association between two variables without considering the cause, whereas the path-coefficient specifies the cause and measures its relative importance (Dewey and Lu, 1959), providing a more adequate view of the genetic association between two traits. However, the present conclusions should be considered with some caution because of the following aspects of the study: a) the study period was relatively short in relation to the culture cycle; b) the conclusions are limited to the genetic material under study; c) genetic sampling was relatively limited in order to obtain sufficiently reliable variance and covariance estimates.

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RESUMO

Estimaram-se as correlações genotípicas e seus desdobramentos em efeitos diretos e indiretos pela análise de caminhamento, entre dez caracteres de plantas adultas de cacau, avaliadas em 12 híbridos, em Medicilândia, PA, em 1987.

Observou-se elevado coeficiente de correlação genotípica entre a altura do fuste e o peso das sementes secas por planta. Contudo, a análise de caminhamento revelou que altura do fuste tem um efeito direto negativo sobre a produção de plantas adultas de cacau.

O número de frutos sadios por planta e o peso das sementes secas por fruto devem ser considerados como os principais componentes de produção uma vez que apresentaram efeitos diretos de elevada magnitude sobre o peso das sementes secas por planta. O número de sementes por fruto e o peso individual de semente seca constituem os principais responsáveis pelo peso das sementes secas por fruto e devem ser considerados como componentes secundários de produção, haja vista que apresentaram efeitos diretos e indiretos de expressiva magnitude.

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