Variability in various agronomic traits of wild cocoa trees (*Theobroma cacao* L.) from the Camopi and Tanpok basins (French Guiana)

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Summary

Variability in various agronomic traits of wild cocoa trees (*Theobroma cacao* L.) from the Camopi and Tanpok basins (French Guiana)

More than 1500 wild cocoa trees (*Theobroma cacao* L.) representing 146 progenies belonging to 11 native populations identified in two river basins were studied individually at CIRAD's Sinnamary station (French Guiana) over a period of 10 years for the following selection criteria: juvenile growth, adult vigour, the production:vigour ratio (cropping efficiency), earliness of production, yields, average pod weight and losses in the field due to rot. For each trait, the variability found in the study material is presented on three levels: individuals, progenies and populations (means, maximum, minimum, coefficients of between-group variation, and mean of the coefficients of within-group variation). A canonical discriminant analysis carried out on seven traits revealed variability structuring that was coherent with the populations defined during surveys.

Key words: Agronomic traits, French Guiana, *Phytophthora*, selection criteria, *Theobroma cacao*, wild cocoa trees

Résumé

Need French title

En collection à la station CIRAD de Sinnamary (Guyane Française), plus de 1500 cacaoyers (*Theobroma cacao* L.) représentant 146 descendances appartenant à 11 populations naturelles locales identifiées dans deux bassins fluviaux, ont été étudiés individuellement pendant 10 ans pour les critères de sélection suivants : la croissance juvénile, la vigueur adulte, le rapport production-vigueur, la précocité de production, la production, le poids moyen d'une cabosse et les pertes par pourritures. Pour chaque descripteur, la variabilité rencontrée dans le matériel étudié est présentée suivant trois niveaux : individus, descendances et populations (moyennes, maximum, minimum, coefficients de variation inter et moyenne des coefficients de variation intra). Une analyse canonique discriminante menée sur sept descripteurs permet de mettre en évidence une structuration de la variabilité cohérente avec les populations définies lors des prospections.

Resumen

Variabilidad de varios rasgos agronómicos del cacao criollo (*Theobroma cacao L.*) de las cuencas del Camopi y del Tanpok (Guinea Francesa)

Más de 1.500 árboles de cacao criollo (*Theobroma cacao L.*), que representan 146 progenies pertenecientes a 11 poblaciones originarias identificadas en dos cuencas rivereñas, se han estudiado individualmente por un periodo de diez años en la estación Sinnamary del CIRAD (Guinea Francesa) según los siguientes criterios de selección: crecimiento juvenil, vigor adulto, producción: porcentaje de vigor (eficacia de siembra), precocidad de producción, cosechas, peso medio de la vaina y pérdidas en el campo a causa de la descomposición. Por cada rasgo, la variabilidad encontrada en el material de estudio se presenta en tres niveles: individuos, progenies y poblaciones (intermedio, máximo, mínimo, coeficientes de variación entre los grupos y promedio de los coeficientes de la variación en el grupo). Un análisis canónico discriminante llevado a cabo sobre siete rasgos ha revelado una variabilidad estructural en perfecta relación con las poblaciones definidas durante los estudios.

Introduction

The wild cocoa trees of southeastern French Guiana (Capperon 1731), were the subject of three surveys between 1987 and 1995 (Lachenaud and Sallée 1993; Lachenaud *et al.* 1997). Studies carried out on this germplasm (Lanaud 1987; Lachenaud and Sallée 1993; Laurent *et al.* 1994; N'goran *et al.* 1994; Sounigo *et al.* 1996, 1999, 20 00; Lachenaud *et al.* 1999, 2000) have revealed its originality within cocoa trees known as 'Forasteros', *T. cacao* subsp. *sphaerocarpum* (Cuatrecasas 1964).

Work on the agronomic evaluation, and the morphological and biochemical characterization of wild Guianan material has been under way since 1988 in Sinnamary, French Guiana, at CIRAD's Paracou-Combi station. The purpose of the research is to provide practical indications to breeders for rational use of this new germplasm. Following a previous article dealing with indications as to origins (populations and/or progenies) to be preferred in breeding programmes (Lachenaud *et al.* 2000), this work uses the complete data to describe the variability found in wild cocoa tree progenies collected in 1987 from the basins of the Tanpok river (upper basin of the Maroni river) and the Camopi river (upper basin of the Oyapok). The traits observed, which were all selection criteria, concerned vigour, earliness, yields, the production:vigour ratio, pod size and resistance in the field to rot diseases (caused locally by various species of *Phytophthora*).

Material and methods

Planting material

At the outset, the planting material studied comprised 146 open-pollinated progenies (i.e. families of seedlings) of wild Guianan cocoa trees, at a rate of a single family (full or half-sibs) per wild mother-tree (i.e. each family came from a pod taken from a wild mother-tree, and each mother-tree was represented by only one family). 144 mother-trees originated from two sub-basins in the far southeast of the country (between 53°27'–53°10'W and 2°19'–2°23'N) and belonged to the following wild populations (Lachenaud and Sallée 1993): Tanpok river (population 5), Camopi river (populations 1, 3, 6, 7, 8, 9, 10, 11, 12, 13).

An additional, non-wild, population, coded '0', comprising two open-pollinated progenies from pods harvested in an old abandoned Amerindian village (near the confluence of the Oyapok and Camopi rivers) was included in the study. As it was probable that the mother-trees in the village were of local origin (Camopi or Oyapok rivers), we kept this 'population' under observation to test that hypothesis. The definition of populations is based primarily on geographical and ecological criteria (Lachenaud and Sallée 1993), and corresponds to the subpopulation ('deme') used by Hartl and Clark (1997). The numbers per population at the time of planting are shown in Table 1. For various reasons (mortality, accidents such as uprooting by the wind, or production constraints imposed by the analyses, etc.), the numbers actually studied were different (Table 2).

Table 1. Distribution by population of wild progenies (Prog.) and of the numbers of trees studied on planting (1988)

Basin	Sub-basin	Population	Prog.	Trees
Oyapok	Camopi	0	2	16
		1	26	274
		3	15	206
		6	1	5
		7	20	209
		8	2	16
		9	50	555
		10	1	12
		11	2	21
		12	10	113
		13	15	176
Maroni	Tanpok	5	2	34
Total			146	1637

The planting design (Lachenaud *et al.* 2000) comprised seven blocks planted in 1988, covering a total area of 0.99 ha. The trees were spaced 3 m x 2 m apart (density of 1667 trees per ha) with a permanent shade of *Gliricidia sepium*, spaced 6 m x 6 m apart. Each block contained 2 to 11 populations, and each population (except "6" and "0") was present in 3–5 blocks. The cocoa trees were monitored individually for 10 years. The edapho-climatic and phytosanitary conditions at the Paracou-Combi station have been described in earlier work (Lachenaud *et al.* 1994).

Methods

Agronomic traits

The agronomic traits chosen for each of the trees (Lachenaud *et al.* 2000) were:

- Juvenile growth, i.e. increase in collar cross-section (=πD^2) (0.15 m from the ground) between 1 and 2 years in the field (=jgr). It was calculated (in cm^2) from two diameter measurements (D) taken with slide callipers.
- Adult vigour, at 10 years (sec98). A circumference measurement was taken 0.50 m from the ground using a tape measure, and a cross-section was calculated (in cm^2).
- Yields, noting for each tree and for each harvesting round the number of healthy pods, their weight, and the number of rotten pods. Accumulated results were used to determine earliness (production in the first 5 years=earliness), as was overall production (cumulated figures up to 10 years). Yields could be expressed as the weight of healthy pods (Wpods) or as a potential (Pot) when rotten pods were taken into account. The equivalence in dry cocoa was obtained by multiplying pod weight (healthy or potential) by the coefficient 0.0875, equal to 0.25 (ratio of fresh pod weight to total pod weight) × 0.35 (ratio of dry cocoa to fresh beans) (Lachenaud *et al.* 1994).
- The production:vigour ratio (i.e. cropping efficiency, in kg of pods × cm^2) was defined as the ratio of potential production accumulated at 10 years to the cross-section measured 0.50 m from the ground at 10 years (=Pot/s).
- The rate of rotten pods. Two parameters could be used: that corresponding to the overall ratio of the number of rotten pods to the total number of pods (or ORR), and that corresponding to the mean of individual values, fixing a minimum yield of 50 pods per tree (=M%R).
- The average pod weight per tree was obtained by the ratio of the accumulated weight of healthy pods to the number of healthy pods (=Wmpod), taking into account only those trees that produced at least 20 healthy pods (Lachenaud *et al.* 2000). This trait is also a morphological descriptor.

Statistical methods

Evaluation

For each of the criteria studied, and for the three levels of variability structuring (overall, populations, progenies), we characterized variability by the following parameters: observed average, maximum and minimum, and coefficient of variation (CV). For the populations and progenies, we give the between-group CV and the mean of the within-group CVs. The within-group CVs were calculated from individual values, whereas the between-group CVs for the progenies or populations were calculated from the mean values (=genetic values) of the progenies and populations. These various CV values illustrate phenotypic variability (overall and within-group) and genetic variability. The discriminant value of each trait was assumed here to be the following ratio: mean of standard deviation within a family (or within a population) : standard deviation between families (or populations). For clones, useful descriptors have a discriminant value below 0.6 (Lachenaud, unpublished data).

Analyses

Initially, an analysis of variance (in unbalanced incomplete blocks, Lachenaud *et al.* 2000) was carried out on the majority of traits, in order to obtain means per progeny fitted to the blocks. Then, to study the structuring of variability in the Guianan germplasm, a canonical discriminant analysis was carried out on the adjusted means of 124 progenies (weighted by the number of individuals), representing eight populations (0, 1, 3, 5, 7, 9, 12 and 13), for seven traits. The eight populations chosen were those that were represented from the beginning to the end of the study (progenies with fewer than 5 trees were withdrawn from the analyses). The seven traits chosen were as follows: juvenile growth, adult vigour, cumulated overall yields (Wpods), the production : vigour ratio, earliness of production, average pod weight and losses in the field from rot. In this case, the average pod weight was a mean per progeny (=total weight of healthy pods produced per progeny : total number of healthy pods) and losses due to rot were an overall ratio per progeny (=total number of rotten pods: total number of pods produced). The canonical discriminant analysis was carried out using the SAS software CANDISC procedure (SAS 1989).

Results

Description of variability

Table 2 shows the variability found in our material for each of the seven traits used. For example, for the usual main selection criterion, potential production, substantial variation was found between progenies, from 0 to 68.4 kg of pods on average per tree. The maximum would seem to correspond to a mean production of 1426 kg of dry cocoa per ha per year, over the first seven harvests. That is a high value for conditions at Paracou-Combi (Lachenaud *et al.* 1994). As for the least variable trait, average pod weight, the progenies nonetheless varied from 200 to 510 g, and the trees from 160 to 600 g. The discriminant values below 0.5 of two traits (juvenile growth and average pod weight) show that these traits might be considered as useful descriptors for the Guianan germplasm.

Canonical discriminant analysis

Wilk's Lambda test was very highly significant (F=4.07 and Proba >F=0.0001): not all the planting material studied was therefore homogeneous for the traits used and the classification into populations by the collectors was therefore valid. The various analysis parameters are given in Table 3, and two planes (axes 1 and 2 and axes 1 and 3) in Figure 1.

The first two axes had a discriminant power equal to 79% of that of the initial seven variables, and the first three axes equal to 96%. Axis 1 was highly correlated with average pod weight and earliness of production, and axis 2 with juvenile growth. For instance, plane 1-2 contrasts populations 7, 1 and 5, which are early yielders, productive, have a high production:vigour ratio and, for 1 and 7, large pods, with the other populations (3, 9, 12 and 0), not very early, not highly productive, with a moderate to low production:vigour ratio, and small pods. Population 13 (low production:vigour ratio and large pods) lies in a central position. The two groups revealed in this way show substantial variability for juvenile growth (axis 2), with population 3 which is highly vigorous when young, unlike 7. Plane 1-3 confirms these differences, grouping together more clearly populations 0, 3, 9, 12 and 13, which are much less variable in relation to axis 3 (mainly correlated with average pod weight) than those in the other group (1–7–5).

Discussion

The experimental variation was rather well controlled in our work, for the model used in the variance analysis (block, popula-

Table 2. Variability for the seven traits studied; where *N*=number of trees, *M*=mean, CV=coefficient of variation (between treatments), MCV=mean of within-group CVs, and D.V.=discriminant value (see text)

	N	*M*	Max.	Min.	CV	MCV	D.V.
1. Juvenile growth (cm²)							
Individuals	1466	12.20	36.63	0.00	57.25		
Progenies	144	11.40	21.90	0.37	39.84	50.82	0.49
Populations	11	12.60	17.42	10.45	21.77	57.24	0.47
2. Adult vigour (cm²)							
Individuals	1470	84.59	323.92	2.96	50.65		
Progenies	143	80.90	131.54	11.77	30.42	43.02	0.50
Populations	12	81.63	94.82	67.33	11.42	49.21	0.79
3. Potential yields (kg of pods)							
Individuals	1470	16.13	184.61	0.00	128.02		
Progenies	143	15.88	68.42	0.00	77.02	101.94	0.57
Populations	12	14.20	22.98	5.37	39.06	122.15	1.15
4. Production:vigour ratio (kg/cm²)							
Individuals	1470	0.158	1.108	0.00	102.65		
Progenies	143	0.159	0.503	0.00	65.57	85.62	0.55
Populations	12	0.144	0.233	0.07	35.03	101.72	0.89
5. Earliness of production (kg)							
Individuals	1548	1.19	45.90	0.00	239.14		
Progenies	145	1.00	8.75	0.00	149.19	203.07	0.87
Populations	12	1.12	3.78	0.00	94.32	234.88	0.84
6. Average pod weight (g)							
Individuals	815	366	600	160	18.13		
Progenies	132	366	510	200	15.03	10.75	0.35
Populations	12	360	425	300	10.92	11.40	0.19
7. Losses through rot (%)							
Individuals	462	1.16	9.62	0.00	139.65		
Progenies	119	1.18	9.21	0.00	100.00	123.54	0.95
Populations	12	1.28	3.05	0.00	69.50	134.30	0.40

Table 3. Factorial discriminant analysis parameters, where *r*=canonical correlation. (For the meaning of the seven variables, see Material and methods)

Axis	*r*	$r^2/(1-r^2)$	Inertia	Between-group correlation with						
				Jgr	Sec98	Early	Pot/s	Wpods	Wmpod	ORR
1	0.728	1.131	0.550	0.173	–0.169	0.875	0.662	0.667	0.876	–0.430
2	0.573	0.490	0.238	–0.949	–0.655	0.251	0.687	0.690	–0.167	0.763
3	0.511	0.354	0.172	0.161	0.279	–0.404	–0.109	0.088	0.447	0.150
4	0.218	0.050	0.024	0.102	0.324	–0.008	–0.196	–0.091	–0.025	0.450

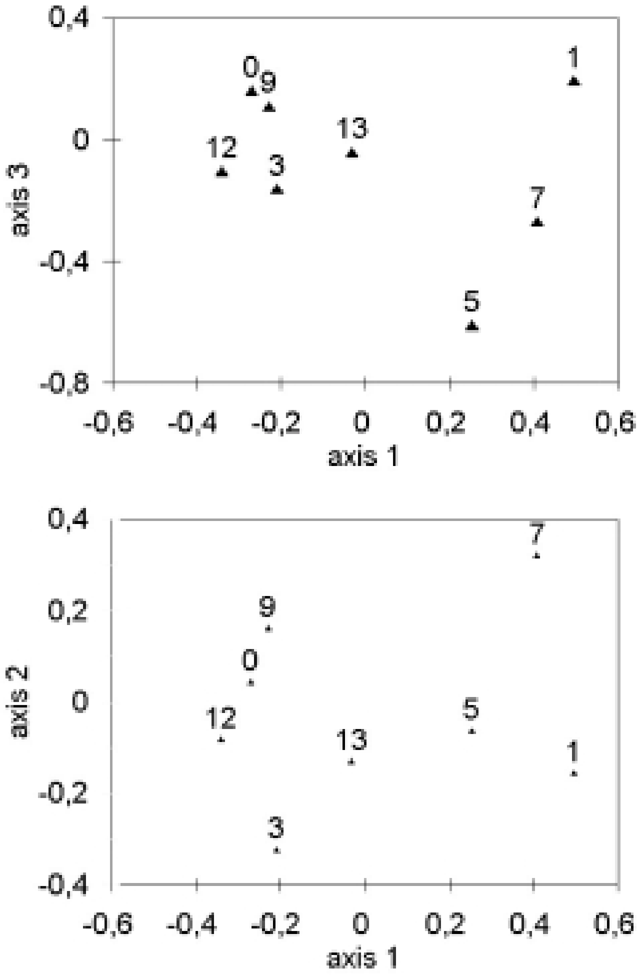

Fig. 1. Representation of the centres of gravity for wild Guianan cocoa tree populations, in the planes of canonical axes 1 and 2 (1a), and 1 and 3 (1b).

tion, progeny in population) explained (in all traits, except losses through rot) 70–89% of the observed variation (Lachenaud *et al.* 2000).

For all traits, the study material revealed notable or substantial variability for the genetic values, illustrated by between-population coefficients of variation of between 11 and 94%, and between-progeny coefficients of variation of between 15 and 149%. The least variable descriptor was average pod weight and the most variable was earliness of production. As the work was not repeated in other locations, there is the theoretical possibility of genotype x location interactions to explain the observed ranking among populations and progenies, but it is unlikely that the extent of variation could be modified..

Unfortunately, these figures cannot be compared with those for other wild populations, as researchers working on similar subjects in Ecuador or Brazil only used morphological descriptors (Allen 1988, Allen and Lass 1983, 1987) or did not present usable data (Barriga *et al.* 1986). Nevertheless, this variability could be compared with that found in an adjacent hybrid trial. This trial, which was also monitored for 10 years, 6 of which were contemporary with the study described here, involved material with a highly diverse pedigree of varied Upper-Amazon, Lower-Amazon and Trinitario origins (Lachenaud *et al.* 1994). For three traits, one chosen for low variability (average pod weight) and the other two for high variability (production potential and rotten pod rate), the between-progeny coefficients of variation (calculated with the same restrictions as regards tree numbers) were 15, 72 and 49% respectively, as opposed to 15, 77 and 100% in the Guianan material.

Phenotypic variability, illustrated by the general CV values between individuals and the means of the within-population and within-progeny coefficients of variation, was also substantial (from 11 to 239%). The mean of the within-population CVs was generally close to the general CV value between individuals, except for average pod weight.

For all traits, the mean of the within-progeny coefficients of variation was slightly lower than the general CV, which reflected the greater homogeneity between sibs or half-sibs. When a comparison was made between the within-progeny coefficients of variation, for the three traits mentioned above, the Guianan material seemed to be more homogeneous than the hybrids: 11, 102 and 123% respectively, as opposed to 19, 116 and 202%.

The between-population CVs were always well below the mean of the within-population CVs (except for average pod weight, where the magnitude found was that observed between trees of the same clone; N'goran 1994), which could indicate that differentiation between populations is quite low, probably due to their large size and/or a not insubstantial flow of genes. It could also be deduced that some of the populations studied may have been geographically less isolated than assumed during the surveys.

In any event, the canonical discriminant analysis confirmed the validity of the classification of Guianan germplasm into populations carried out by the collectors in 1987, based on geographical (remoteness and isolation) and ecological criteria. This analysis brought out two main groups: the first contained populations 1, 5 and 7 and the second populations 3, 9, 12, 13 and 0. The first group could be qualified as the 'upstream' group (upstream of the Camopi basin and part adjacent to the Tanpok basin) and the second the 'downstream' group, with the boundary between the upstream and downstream groups marked by the mountain known as Montagne Cacao (Lachenaud and Sallée 1993). However, populations 1, 5 and 7 were clearly individualized, while the other populations seemed to be less differentiated. Population 0, derived from mother-trees 'domesticated' at one time by the Amerindians, was similar to 9, and our results tally with the hypothesis of a local origin. Population 9 was the population located furthest downstream, and therefore nearest to Camopi. It was also the largest, and extended over both banks of the river. It is therefore plausible that Amerindians brought back pods to the village from a trip up the Camopi, not to cultivate cocoa trees, but as a dainty for their children. A few seedlings could have survived from seeds discarded here and there.

The structuring revealed by this study confirms the difference already noted, including *in situ*, between populations 1 and 7 on the one hand and 3, 9, 12 and 13 on the other hand for certain pod descriptors (Lachenaud and Sallée 1993) and floral descriptors (Lachenaud *et al.* 1999). The populations from the Camopi basin are therefore not a homogeneous set, and quite small distances (as the crow flies) seem to isolate certain populations, such as populations 1 and 13. Although these two populations are only 1000 metres apart, they are not in communication via the Camopi river, and the Montagne Cacao lies between them. Likewise, populations 3 and 9, which are only separated by the river known as Crique Cacao (a tributary of the Camopi) seem to be distinct from each other, particularly in plane 1×2. These results show that the variability of the wild cocoa tree populations is not structured solely by the river basin to which they belong, but that other factors must be involved, such as reproductive isolation, the numerical size of the populations and their geographical remoteness (Lachenaud *et al*. 1999).

Agronomic traits (with the exception of average pod weight, which is also a morphological descriptor) are not usually considered as useful descriptors, for they are very time-consuming. However, our results show that juvenile growth, with a discriminant value below 0.6, could also be used, at least for the Guianan germplasm.

Conclusion

The wild cocoa trees of French Guiana, which form a particular group, have yet to be used in cocoa breeding, though certain origins have already been disseminated, sometimes widely, to numerous producing countries. It is therefore important to facilitate their use by evaluations and characterizations accessible to researchers, and by studies showing how variability is structured in this group, as despite the routine use of molecular markers in recent years, using morphological and agronomic descriptors remains worthwhile and necessary, in genetic diversity studies too (Sounigo *et al*. 1997).This work is a contribution to the second aspect.

The variability discovered for seven agronomic traits from among the main selection criteria (vigour, productivity, cropping efficiency, pod size and performance with respect to rot diseases) is substantial, for both phenotypic and genetic values. A canonical discriminant analysis involving seven traits, carried out on 124 progenies representing eight populations, showed that the genetic structuring of the study material tallied with the different wild populations identified by the collectors. These results confirm and fine-tune those obtained with other descriptors (Lachenaud *et al.* 1999), while showing the potential discriminant value of a set of agronomic traits.

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