# Agronomic assessment of wild cocoa trees (*Theobroma cacao* L.) from the Camopi and Tanpok basins (French Guiana)

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## Summary

**Agronomic assessment of wild cocoa trees (*Theobroma cacao* L.) from the Camopi and Tanpok basins (French Guiana)**

A study was made of around 1600 individual cocoa trees (*Theobroma cacao* L.) representing 144 open-pollinated progenies and 11 wild populations identified in two river basins of French Guiana, based on the following selection criteria: juvenile growth (or vigour), adult vigour, the yield:vigour ratio, earliness of production, yield, average pod weight and losses due to rot in the field. Observations were carried out at CIRAD's Sinnamary station in French Guiana over a total of 10 years. The analysis of variance carried out on the seven most numerous populations (amounting to 97% of the individuals) revealed population and/or progeny effects for all the criteria. It is proposed that the study material be incorporated into genetic improvement programmes, particularly for yield, the yield:vigour ratio and performance in the field with respect to rot diseases. To that end, practical indications are given to breeders for choosing from the populations and progenies.

**Key words**: Characterization, descriptors, French Guiana, genetic improvement, *Phytophthora*, populations, *Theobroma cacao*, wild cocoa trees

**Abbreviation:** CIRAD: Centre de Coopération Internationale en Recherche Agronomique pour le Développement (Montpellier, France)

## Résumé

**Evaluation agronomique des cacaoyers spontanés (*Theobroma cacao* L.) des bassins du Camopi et du Tanpok (Guyane Française)**

Environ 1600 cacaoyers (*Theobroma cacao* L.) représentant 144 descendances libres appartenant à 11 populations naturelles identifiées dans deux bassins fluviaux de Guyane Française, ont été étudiés individuellement pour les critères de sélection suivants : la croissance (ou vigueur) 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 au champ. Les observations ont été réalisées à la station CIRAD de Sinnamary en Guyane, sur une durée totale de 10 ans. L'analyse de la variance, effectuée sur les 7 populations les plus nombreuses (représentant 97% des individus) permet de mettre en évidence des effets "population" et/ou "descendance" pour tous les critères. Il est proposé d'intégrer le matériel étudié dans les programmes d'amélioration génétique, particulièrement pour les critères de production, de rapport Production / Vigueur et de comportement vis-à-vis des pourritures au champ. Dans ce but, des indications pratiques sont données aux sélectionneurs quant aux populations et descendances à préférer.

## Resumen

**Evaluación económica de cacao silvestre (*Theobroma cacao* L.) de las cuencas de Camopi y Tanpok (Guayana Francesa)**

Se hizo un estudio de unos 1600 ejemplares de árboles de cacao (*Theobroma cacao* L.) representativos de 144 linajes de polinización abierta y 11 poblaciones silvestres identificados en dos cuencas fluviales de Guayana Francesa, con los siguientes criterios de selección: crecimiento (o vigor) juvenil, vigor adulto; relación rendimiento-vigor, precocidad de producción, rendimiento, peso medio de la vaina y pérdidas por podredumbre en el campo. Las observaciones se realizaron en la estación Sinamary del CIRAD en la Guayana Francesa a lo largo de 10 años. El análisis de varianza realizado en las siete poblaciones más numerosas (que contienen el 97% de los árboles) reveló los efectos sobre la población y/o el linaje según todos los criterios. Se propone que el material del estudio se incorpore a programas de mejoramiento genético, en particular en atención al rendimiento, la relación rendimiento-vigor y los resultados en el campo respecto a las enfermedades de podredumbre. Con ese fin, se dan indicaciones prácticas a los fitogenetistas para escoger entre poblaciones y linajes.

## Introduction

The wild cocoa trees of southeastern French Guiana, which have been known to exist since 1729 (Capperon, 1731; Leconte and Challot 1897), have been surveyed and collected on three occasions in 1987, 1990 and 1995 (Lachenaud and Sallée 1993; Lachenaud *et al.* 1997). Numerous studies of this germplasm since 1987 (Lanaud 1987; Lachenaud and Sallée 1993; Laurent *et al.* 1994; N'Goran *et al.* 1994; Lachenaud *et al.* 1997; Sounigo *et al.* 1996, 1999; Lachenaud *et al.* 1999) have all revealed its uniqueness among 'Forastero' cocoa trees (*T. cacao* subsp. *sphaerocarpum*) (Cuatrecasas 1964). This uniqueness is such that this group of cocoa trees is now considered one of the four poles of the species' genetic structuring (Lachenaud 1997; Lanaud *et al.* 1999). Nevertheless, before it can be used for genetic improvement, it needs to be described, characterized and evaluated, particularly for selection criteria.

Agronomic and morphological characterization of this wild Guianan material has been under way since 1988 near Sinnamary, French Guiana, where the Paracou-Combi reference collection is planted. The aim is twofold: to gain further knowledge of variability in this original material and identify origins (populations or families) that are potentially useful in breeding, and to provide practical indications for breeders who wish to use them. This article covers only the latter aspect. It presents the results of 10 years' agronomic assessment of progenies from wild cocoa trees collected in 1987 in the basins of the Tanpok river (upper basin of the Maroni river) and the Camopi river (upper basin of the Oyapok). The traits used, which are all selection criteria, were vigour, earliness of production, yield, the yield:vigour ratio, pod size and resistance to rot (caused by various species of *Phytophthora*) in the field.

## Material and methods

### Planting material

The planting material studied at the outset comprised 144 open-pollinated progenies of wild cocoa trees. Each progeny came from a pod taken from a wild mother-tree, and each mother-tree was represented by only one progeny. The 144 mother-trees originated from two subbasins in the far southeast of the country (between 53°27' and 53°10' W and 2°19' and 2°23' N). Trees collected in the Camopi basin belonged to wild populations 1, 3, 6, 7, 8, 9, 10, 11, 12 and 13, while those collected in the Tanpok basin belonged to wild population 5 (Lachenaud and Sallée 1993). The population concept used here was that used by Pernes (1984) and Berthaud (1986) for coffee trees, and corresponds to the subpopulation ('deme') referred to by Hartl and Clark (1997).

The number of trees per population (on planting and at the end of the study) is shown in Table 1. On planting, the number varied from 2 to 19 trees per progeny, with an average of 11.2. The trees were planted between January and June 1988 in seven blocks in two plots either side of a small bottomland, over a total area of 0.99 ha. The trees were planted 3 m x 2 m apart, corrresponding to a density of 1667 plants/ha. The cocoa seedlings were planted under temporary banana shade (at the same density) for 4 years. The permanent shading was provided by *Gliricidia* sp., spaced 6 m x 6 m apart. The blocks received mineral fertilization of the 'soil diagnosis' type (Jadin and Snoeck 1985), supplemented with applications of nitrogen and boron. Each block contained 2 to 11 populations and each population analyzed was present in three to five blocks. The seven blocks were monitored for 10 years. The trial did not have integrated controls representing other groups of cocoa trees, such as Upper or Lower Amazon Forasteros or Trinitrarios. Nevertheless, in some cases, orders of magnitude could be obtained from the results of an adjacent hybrid comparative trial (plot C0) also monitored for 10 years, six of which were contemporary with the study in question (Lachenaud *et al.* 1994). The edapho-climatic and phytosanitary conditions at the Paracou-Combi station have been described in earlier work (Lachenaud *et al.* 1994).

### Agronomic descriptors

The agronomic descriptors chosen for each of the trees were as follows:

- Juvenile growth, i.e. the increase in 'collar' cross-section (15 cm from the ground) between 1 and 2 years in the field. This was calculated (in $cm^2$) from two diameters measured with slide calipers.
- Adult vigour. The circumference of the tree at 10 years old was measured 50 cm from the ground with a tape measure and a cross-section calculated (in $cm^2$).
- Yield. This was calculated from the number of healthy pods, their weight and the number of rotten pods (without specifying the causal agent) for each tree and each harvesting round. Earliness of production and overall yield were obtained by cumulating the figures. Final yield was expressed as the weight of healthy pods, or as a potential yield if rotten pods were taken into account. The dry cocoa equivalent was calculated by multiplying pod weight (healthy or total) by a coefficent of 0.0875, equal to 0.25 (ratio of fresh bean weight to pod weight) x 0.35 (ratio of dry cocoa to fresh beans) (Lachenaud *et al.* 1994).
- Yield:vigour ratio. This is the ratio of potential yield cumulated at 10 years to the cross-section 50 cm from the ground at 10 years. It was therefore expressed as kg of pods per $cm^2$.
- Average pod weight. The average weight of one pod per tree was calculated from the ratio of cumulated healthy pod weight to the number of healthy pods, keeping only those trees that produced at least 20 healthy pods, a quantity which enabled characterization of a tree for this criterion (N'Goran 1994).
- Losses due to rot diseases. The rate of rotten pods per tree was determined by counting. The analysis results were means (per population or per progeny) of individual rates, taking a minimum yield of 50 pods per tree. This is quite a high value but was necessary given the low rotten pod percentages. A study of correlations (not shown) revealed that this parameter was well correlated to the overall rate per population or per progeny (total rotten pods/total pods).

**Table 1. Distribution by population of open-pollinated progenies (OP) and trees studied, on planting (1988) and after monitoring for 10 years (1997)**

| | | | 1988 | | 1997 | |
|---|---|---|---|---|---|---|
| Basin | Subbasin | Population | OP | Trees | OP | Trees |
| Oyapok | Camopi | 1 | 26 | 274 | 26 | 256 |
| | | 3 | 15 | 206 | 15 | 187 |
| | | 6 | 1 | 5 | 1 | 5 |
| | | 7 | 20 | 209 | 19 | 168 |
| | | 8 | 2 | 16 | 2 | 11 |
| | | 9 | 50 | 555 | 50 | 510 |
| | | 10 | 1 | 12 | 1 | 12 |
| | | 11 | 2 | 21 | 1 | 9 |
| | | 12 | 10 | 113 | 10 | 101 |
| | | 13 | 15 | 176 | 15 | 162 |
| Maroni | Tanpok | 5 | 2 | 34 | 2 | 33 |
| Totals | | | 144 | 1621 | 142 | 1454 |

### Statistical methods

The design of the collection lent itself to an analysis in unbalanced incomplete blocks. The analysis of variance was carried out on data from micro-plots of varying sizes (from 1 to 10 trees), which were progeny-block combinations. The fixed effects model used was as follows:

$Y_{ijk} = \mu + B_i + P_j + D_k(P_j) + \varepsilon_{ijk}$

where $Y_{ijk}$ = the mean for the micro-plot of progeny k, population j, block i
$\mu$ = overall mean
$B_i$ = effect of block i
$P_j$ = effect of population j
$D_k(P_j)$ = effect of progeny k in population j
$\varepsilon_{ijk}$ = residual random error

The overall means per population, or per progeny, resulted from an adjustment to the blocks, and weighting by the numbers of trees in the microplots.

The analyses of variance were carried out with the SAS software GLM procedure, using the LSMEANS option (SAS 1989). In the absence of a way to ensure the validity of the analyses of variance carried out in this particular case, the main criterion adopted was homogeneity of the within-population variances of the residuals (the raw residuals multiplied by the square root of the numbers of trees in the microplots), using Levene's test at 5%. In the event of heterogeneity, the responsible populations were excluded from the analyses (Table 2). Normality of the model residuals was also checked using Shapiro-Wilk's W test. However, owing to the large numbers studied and the robustness of the analysis of variance compared to the deviations from the norm, the formal non-normality of the model residuals was not a problem, provided the distribution approximately followed a 'bell' curve. The results shown (*cf.* Table 3) were obtained by analyses that verified those criteria.

If the population and/or progeny effects were significant, the adjusted means were compared (2 by 2 by a Student's t-test) and a synthesis is shown (Table 2). For the progenies, given the large numbers involved, comparisons were made only with the mean progeny (the progeny whose performance was equivalent to the mean of those progenies included in the analysis; the progeny used varied depending on the descriptor), and the means could be classed in three groups: worse than, equal to, or better than the mean progeny. Only the seven most represented populations (1, 3, 5, 7, 9, 12 and 13, i.e. 97.4% of the trees at 10 years) were analyzed. In principle, progenies with fewer than five trees were always taken out of the analyses.

## Results

### *Juvenile growth*

The analysis of variance revealed very highly significant block, population and progeny effects (probability > F = 0.0001). The overall model effect was also very highly significant ($R^2$=0.89). Classification of the populations according to their adjusted means (in $cm^2$) is shown in Table 2.

Twelve progenies were statistically inferior to the mean of the population, and 11 better. In increasing order of growth, the best five progenies were GU 186, 238, 340, 287 and 264. The worst five progenies, in decreasing order of growth, were GU 291, 313, 350, 354 and 126.

### *Adult vigour*

The analysis of variance revealed a very highly significant model effect ($R^2$=0.81), along with block, population and progeny effects that were also very highly significant. The population means (in $cm^2$) could be classed in two groups (Table 2). Eleven progenies were worse than the mean progeny, and 9 better. The five most vigorous families were GU 163, 174, 285, 323 and 178, whilst the five least vigorous families were GU 350, 304, 344, 345 and 313.

### *Yield*

Given the strong correlations between the different yield descriptors (not shown), only the 'potential' variable was analyzed. The analysis of variance revealed a very highly significant model effect ($R^2$=0.75). The population effect was not significant, but progeny and block effects were very highly significant. Exclusion of population 7 from the analysis could explain the lack of a population effect despite the high amplitude of the adjusted means between well represented populations (from 11.1 kg of pods for population 3 to 20.4 for population 7). Four progenies gave significantly lower yields than the mean progeny, and 14 gave higher yields. In increasing order, the five highest yielding progenies were GU 134, 280, 143, 303 and 285. The five lowest yielding progenies were GU 244, 250, 222, 113 and 282.

### *Yield:vigour ratio*

The analysis of variance revealed a very highly significant model effect ($R^2$=0.73). The population effect was not significant (prob-

**Table 2. Means (adjusted to the blocks) of seven main populations (and plot means) for seven traits. The values indicated for potential yield, potential yield/cross-section and earliness are in kg of pods**

| Population | Juvenile growth ($cm^2$) | Adult vigour ($cm^2$) | Potential yield (kg/tree) | Potential yield/ cross-section (kg /$cm^2$) | Earliness (kg/tree) | Average pod weight (g) | % rot |
|---|---|---|---|---|---|---|---|
| 1 | 13.8 a | 87.7 a | 18.2 a | 0.17 a | 1.2 ab | 435 a | 1.3 bc |
| 3 | 13.5 ab | 87.4 a | 11.1 a | 0.11 a | 0.8 ab | 322 d | 1.4 bc |
| 5 | 13.4 abc | 85.2 ab | 14.9 a | 0.14 a | 2.6 * | 351 c | 3.6 a |
| 7 | 10.2 d | 75.7 b | 20.4 * | 0.21 * | 3.0 * | 380 b | 1.6 b |
| 9 | 11.6 cd | 83.2 ab | 15.7 a | 0.15 a | 1.2 ab | 359 c | 1.0 bc |
| 12 | 12.1 bc | 88.1 a | 16.1 a | 0.17 a | 0.6 b | 316 d | 1.2 bc |
| 13 | 12.7 abc | 82.6 ab | 16.9 a | 0.17 a | 1.3 a | 386 b | 0.6 c |
| Mean | 12.3 | 85.1 | 16.4 | 0.16 | 1.2 | 367 | 1.2 |

* = population taken out of the analysis to satisfy homogeneity of within-population variances.
Means followed by the same letter are not significantly different (P<0.05).

ably due to the exclusion of population 7), but progeny and block effects were very highly significant. Six progenies were significantly worse than the mean progeny and 12 were better. The best five were GU 325, 139, 285, 303 and 134; the worst five were GU 313, 194, 250, 113 and 282.

### *Earliness of production*

In order to carry out a valid analysis of variance, the two most precocious populations, 5 and 7, had to be excluded. On the remaining sample (5 populations, 107 progenies), the analysis revealed a very highly significant model effect ($R^2 = 0.70$), a significant population effect and very highly significant block and progeny effects. Based on their (adjusted) yield the populations could be classed in two homogeneous groups (Table 2). The best five were GU 146, 116, 139, 143 and 134. Twenty-eight progenies (out of 143), 21 of which were represented by at least five trees, did not produce a single pod for five years.

### *Average pod weight*

Considering only those trees that produced at least 20 healthy pods, forty-eight progenies were excluded from the analysis of variance. The model was very highly significant ($R^2$=0.88), as were the effects considered, particularly the population effect (F=44.0). Classification of the means revealed four separate groups (Table 2). Sixteen progenies were significantly better than the mean progeny and 19 worse. The progenies with the heaviest pods were GU 157, 161, 274, 212 and 285. Those with the smallest pods were GU 311, 162, 218, 205 and 230.

### *Losses due to rot diseases*

Fixing yield at 50 pods per tree substantially reduced the number of trees to be studied, along with the number of satisfactorily represented progenies (only 42 out of the 142 progenies had five trees or more). We therefore simplified the model, keeping only the population and block effects for the analysis of variance (and using arc sine square root transformation of the rotten pod rate to normalize the residuals). The model was very highly significant (but $R^2$ was only 0.18), as were the population and block effects. The population means could be classed in three groups (Table 2). The five progenies (with at least five trees) with fewest losses due to rot diseases were GU 252, 321, 325, 134 and 240 (from 0.52 to 0.13%). The progenies with the greatest losses were GU 186, 157, 129, 146 and 116 (from 2.10 to 3.05%).

## Discussion

The analysis of variance revealed significant population and/or progeny effects that, along with the degree of variability noted for most of the traits, provide for effective selection. Although our results were obtained in only a single environment, they should help geneticists who have Guianan material at their disposal, or who wish to acquire it, to make selections. To facilitate that selection, Table 3 provides a list of the populations and progenies, and Table 4 indicates the correspondence between the material mentioned in this article and the sib material (half or full sibs, derived from pods collected from the same mother-trees) already supplied to several producing countries. CIRAD has been supplying GU clonal material on request to countries or institutions from its quarantine centre in Montpellier since 1989 (Lachenaud and Sallée 1993). More recently, this material has been supplied from quarantine centres at the University of Reading, UK and the Trinidad Cocoa Research Unit in Barbados.

The following comments can be made regarding the main descriptors:

- Yield:vigour ratio. Population 7 is the best population for this paramount selection criterion in cocoa improvement (Lotodé and Lachenaud 1988; Paulin *et al.* 1993). Two progenies (GU 134 and GU 303) gave better values than those scored by the best progeny

Table 3. **Distribution of GU progenies by population**

| Population | GU progeny |
|---|---|
| 1 | 116, 156 to 161 and 250 to 286 |
| 3 | 218 to 241 and 347 to 349 |
| 5 | 113 to 116 and 123 |
| 7 | 126 to 152 |
| 9 | 162 to 198, 242 to 249, 297 to 330 and 350 to 355 |
| 12 | 203 to 217 |
| 13 | 287 to 295 and 331 to 346 |

**Table 4. Correspondence between the GU progenies mentioned in this article (A) and those supplied to producing countries and quarantine centres (B)**

| A | B | A | B | A | B | A | B |
|---|---|---|---|---|---|---|---|
| GU 113 | GU 114 | GU 174 | GU 175 | GU 250 | GU 251 | GU 313 | GU 314 |
| GU 116 | - | GU 178 | GU 179 | GU 252 | GU 253 | GU 321 | GU 322 |
| GU 126 | - | GU 186 | - | GU 264 | GU 265 | GU 323 | GU 324 |
| GU 129 | - | GU 194 | GU 195 | GU 274 | GU 275 | GU 325 | - |
| GU 134 | - | GU 205 | - | GU 280 | GU 281 | GU 340 | GU 341 |
| GU 139 | GU 140 | GU 212 | GU 213 | GU 282 | - | GU 344 | - |
| GU 143 | GU 144 | GU 218 | GU 219 | GU 285 | GU 286 | GU 345 | GU 346 |
| GU 146 | GU 147 | GU 222 | - | GU 287 | GU 288 | GU 350 | GU 351 |
| GU 157 | GU 158 | GU 230 | GU 231 | GU 291 | - | GU 354 | GU 355 |
| GU 161 | - | GU 238 | GU 239 | GU 303 | - | | |
| GU 162 | - | GU 240 | GU 241 | GU 304 | GU 305 | | |
| GU 163 | GU 164 | GU 244 | - | GU 311 | GU 312 | | |

- = no corresponding material outside French Guiana.

(UPA 402 x UF 676) in the neighbouring hybrid trial. Given its poor yield:vigour ratio, population 3 should be ruled out for further selection.

- Earliness of production. The average precocity of the study material was low and well below that of the hybrid material in the adjacent trial. However, some blocks suffered considerably from thrips (*Selenothrips rubrocinctus*) attacks in the first three years, which affected juvenile growth and probably delayed the start of bearing. This may explain the low correlations seen between the juvenile and adult criteria. The most precocious population was 7, followed by 5 (the only one originating from the Tanpok basin). The best progeny produced the equivalent of 1275 kg of dry cocoa per hectare, cumulated over five years, which was similar to the mean for neighbouring trial C0. Population 12 seemed to be particularly late.
- Yield. The yields of the populations or progenies varied considerably. The best populations seemed to be 7 and 1, and the worst 3. Over seven seasons, the best progeny produced an annual mean yield of 1426 kg of dry cocoa per ha, which would have put it in second place in hybrid trial C0 (Lachenaud *et al.* 1994). The best progenies produced yields approaching 3000 kg of dry cocoa per hectare once in full production (Table 5), i.e. more than the best hybrid progenies in C0. It should be noted that these yields are potential yields, but similar to actual yields given the good overall performance of Guianan material in relation to rot diseases, and the seven blocks studied had permanent *Gliricidia* shading, unlike hybrid trial C0 which was unshaded. In contrast, some progenies seemed to be almost or totally sterile, with mean yields of 0 to 15 pods per tree over 10 years. These low-yielding progenies also showed poor vegetative development and low yield:vigour ratios (from 0.00 to 0.04). For instance, the seven trees of progeny GU 313 had an average cross-section of 11.8 cm$^2$ in 1998 and did not produce a single pod in 10 years. This reveals the need for multi-site trials, as the mother-tree of this progeny achieved substantial vegetative development in its wild state, with a height of 20 m.
- Average pod weight. When applying a minimum yield of 20 healthy pods per tree, average pod weight seemed to be the least variable criterion of all those studied. However, the differences between populations were clear and significant, and also confirmed observations *in situ* (Lachenaud and Sallée 1993). Population 1 produced the heaviest pods, followed by 13 and 7. Some trees, and even one progeny, were found to produce an average pod weight of over 500 g (up to 600 g), which is high given that all the healthy pods were taken into account.
- Losses caused by rot diseases were negligible at only 1.15% of pods for the trial as a whole. Losses varied from 0 to 3% per population, and from 0.0 to 9.2% per progeny. The highest individual value was 9.6%. In comparison, overall losses in the C0 trial were 4.7%, with a range of 1.0 to 8.7% per progeny and an individual maximum of 25.0%. Thus Guianan material in this trial had high overall levels of tolerance to rot diseases. Twenty-four high-yielding trees (more than 200 pods) with rot rates lower than or equal to 1% could be cloned. The population from Tanpok was significantly more susceptible to rot diseases than were he Camopi populations.

## Conclusion

Despite the routine use of molecular markers in recent years, using morphological and agronomic descriptors in genetic diversity studies is still worthwhile and necessary (Sounigo *et al.* 1997). Indeed, in the absence of QTLs, agronomic descriptors are still irreplaceable when choosing parents to be incorporated into breeding programmes. The wild cocoa trees of French Guiana form a special group and have yet to be used in cocoa breeding. As they have been distributed to numerous countries, it is important to facilitiate their use through characterizations and assessments accessible to researchers. The agronomic characteristics of wild material from the Camopi and Tanpok basins that we have just described reveal noteworthy performances of certain progenies, or even populations, particularly as regards yield, the yield:vigour ratio and resistance to rot diseases. Based on this, we recommend their use in genetic improvement programmes, and the practical indications provided by this study (populations and progenies) should assist breeders in selecting breeding material.

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## References

Berthaud, J. 1986. Les ressources génétiques pour l'amélioration

Table 5. Mean and maximum potential yields from year 6 to year 10 for the first four blocks in the trial and potential yields of progenies GU 244 (very poor), GU 291 (poor), GU 280 (good). The data are in kg of pods per tree and, in brackets, in kg of dry cocoa per hectare

| | Year 6 (1993) | Year 7 (1994) | Year 8 (1995) | Year 9 (1996) | Year 10 (1997) |
|---|---|---|---|---|---|
| Mean | 2.42 | 1.51 | 4.74 | 2.40 | 2.95 |
| | (353) | (220) | (691) | (350) | (430) |
| Max. | 10.91 | 7.69 | 20.29 | 11.60 | 19.92 |
| | (1591) | (1122) | (2960) | (1692) | (2906) |
| GU 244 | 0.00 | 0.00 | 0.09 | 0.11 | 0.51 |
| GU 291 | 0.18 | 0.25 | 1.16 | 0.09 | 0.40 |
| GU 280 | 6.91 | 5.58 | 14.91 | 6.50 | 10.37 |
| | (1008) | (814) | (2175) | (948) | (1513) |

des caféiers africains diploïdes. Editions de l'ORSTOM, collection 'Travaux et documents' 188. 379 pp.
Capperon. 1731. Journal de voyage du haut de la rivière du Camaupi pour la découverte du cacao et salsepareille faite par le sieur Capperon, capitaine d'une compagnie de la garnison de Cayenne et commandant sous le Roy du fort d'Oyapok. Archives départementales de Guyane, C14, Reg. 15, 1731:112-121.
Cuatrecasas, J. 1964. Cacao and its allies. A taxonomic revision of the genus *Theobroma*. Contrib. US Nat. Herbarium 35(6). Smithsonian Institution, Washington, DC, USA.
Hartl, D. L. and A.G. Clark. 1997. Principles of population genetics. Third edition. Sinauer Associates, Sunderland, Massachusetts, USA.
Jadin, P. et J. Snoeck. 1985. La méthode du 'diagnostic-sol' pour calculer les besoins en engrais des cacaoyers. Café, Cacao, Thé 29(4):255-266.
Lachenaud, Ph. 1997. Genetic/taxonomic structuring of the *Theobroma cacao* L. species. Fresh hypotheses. Ingenic Newsl. 3:10-11.
Lachenaud, Ph., F. Bonnot and G. Oliver. 1999. Use of floral descriptors to study variability in wild cocoa trees (*Theobroma cacao* L.) in French Guiana. Genet. Resour. Crop Ev. 46:491-500.
Lachenaud, Ph., D. Clement, B. Sallée et Ph. Bastide. 1994. Le comportement en Guyane de cacaoyers sélectionnés en Côte d'Ivoire. Café, Cacao, Thé 38(2):91-102.
Lachenaud, Ph. , V. Mooleedhar and C. Couturier. 1997. Wild cocoa trees in French Guiana. New surveys. Plantations, recherche, développement 4(1):25-32.
Lachenaud, Ph. et B. Sallée. 1993. Les cacaoyers spontanés de Guyane. Localisation, écologie, morphologie. Café, Cacao, Thé 37(2):101-114.
Lanaud, C. 1987. Nouvelles données sur la biologie du cacaoyer (*Theobroma cacao* L.). Thèse de doctorat d'état. Université de Paris XI, Orsay, France. 262 pp.
Lanaud, C., J.-C. Motomayor et O. Sounigo. 1999. Le cacaoyer. *In* Diversité génétique des plantes tropicales cultivées (P. Hamon, M. Seguin, X. Perrier et J.C. Glaszmann, eds.). CIRAD, Montpellier, France. 387 pp.
Laurent, V., A.M. Risterucci and C. Lanaud. 1994. Genetic diversity in cocoa revealed by cDNA probes. Theor. Appl. Gen. 88:193-198.
Leconte, H. et C. Challot. 1897. Le cacaoyer et sa culture. G. Carré et C. Naud, éditeurs, Paris, France. 121 pp.
Lotodé, R. et Ph. Lachenaud. 1988. Méthodologie destinée aux essais de sélection du cacaoyer. Café, Cacao, Thé 32(4):275-292.
N'Goran, J.A.K. 1994. Contribution à l'étude génétique du cacaoyer par les marqueurs moléculaires: diversité génétique et recherche de QTLs. Thèse de doctorat. Université de Montpellier II, France. 105 pp.
N'Goran, J.A.K., V. Laurent, A.-M. Risterucci and C. Lanaud. 1994. Comparative genetic diversity studies of *Theobroma cacao* L. using RFLP and RAPD markers. *Heredity* 73:589-597.
Paulin, D., G. Mossu, Ph. Lachenaud et C. Cilas. 1993. La sélection du cacaoyer en Côte d'Ivoire. Analyse du comportement de soixante deux hybrides dans quatre localités. Café, Cacao, Thé 37(1):3-20.
Pernes, J. 1984. Gestion des ressources génétiques des plantes. Tome 1: monographies. Technique et Documentation, Lavoisier, Paris, France.
SAS Institute. 1989. SAS/STAT User's Guide, Version 6. Fourth Edition, 1 & 2. SAS Institute, Cary, NC, USA.
Sounigo, O., F. Bekele, G. Bidaisee, Y. Christopher et R. Umaharan. 1997. Comparison between genetic diversity data obtained from morphological, biochemical and molecular studies. Pp. 20-29 *in* Cocoa Research Unit, Report for 1997. The University of the West Indies, St Augustine, Trinidad.
Sounigo, O., Y. Christopher and R. Umaharan. 1996. Genetic diversity assessment of *Theobroma cacao* L. using iso-enzyme and RAPD analyses. Pp. 35-51 *in* Cocoa Research Unit, Report for 1996. The University of the West Indies, St Augustine, Trinidad.
Sounigo, O., S. Ramdahin, R. Umaharan and Y. Christopher. 1999. Assessing cacao genetic diversity using IE and RAPD techniques. Pp. 25-28 *in* Cocoa Research Unit, Annual Report 1998. The University of the West Indies, St Augustine, Trinidad.