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Review

Twenty years of agronomic evaluation of wild cocoa trees (*Theobroma cacao* L.) from French Guiana

Ph. Lachenaud [a,*], D. Paulin [a], M. Ducamp [b], J.-M. Thevenin [a]

[a] *CIRAD-Bios, UPR "Bioagresseurs de Pérennes", TA-A31/02, 34398 Montpellier Cedex 5, France*
[b] *CIRAD-Bios, UMR BGPI, TA-A54/K, 34398 Montpellier Cedex 5, France*

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Abstract

Almost 500 clones of wild cocoa trees (*Theobroma cacao* L.) grown from pods collected in 1987 from wild mother-trees in the Camopi and Tanpok river basins (southeastern French Guiana) have been distributed in around fifteen cocoa producing countries since 1988. The name of those clones always bears the GU prefix (for "Guyane", i.e. French Guiana). All the germplasm of the same geographical origin present in the CIRAD collection at Paracou-Combi (Sinnamary, French Guiana), i.e. more than 1600 trees, has been abundantly studied for its morphological characterization, its agronomic assessment or its genetic diversity. Other assessment work, primarily on resistance to certain diseases, has been carried out by CIRAD in Montpellier, or in various countries by other organizations.

In order to simplify the choice for breeders faced with a large number of GU clones and wishing to use some of them, an overview is presented here of the results obtained with this germplasm for various selection criteria such as productivity, the yield:vigour ratio (cropping efficiency), pod filling, bean size, resistance to pests and diseases, compatibility, sensory qualities, etc. The results obtained for resistance of this material to witches' broom disease and black pod rot show a globally high level of resistance, making the GU germplasm a new and major potential source of resistance to those diseases. The same seems to apply for resistance to mirid damage. The yield levels achieved in French Guiana, along with cropping efficiency, are noteworthy in some families. The first results acquired reveal a substantial heterosis effect when GU clones are hybridized with other groups.

Given their distribution in several countries, the known individual qualities and performance of some GU clones present at the Reading quarantine station (UK) are indicated. A selection of clones that are of interest or promising for incorporation in breeding programmes is provided for each criterion.

Keywords: Agronomic traits; Cocoa; French Guiana; Leaf test; *Moniliophthora*; *Phytophthora*

Contents

* Corresponding author. Tel.: +33 4 67 71 56 33; fax: +33 4 67 61 55 81.
E-mail address: philippe.lachenaud@cirad.fr (P. Lachenaud).

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1. Introduction

The cocoa tree (*Theobroma cacao* L., Malvaceae, formerly Sterculiaceae) is a tree that originates from the neotropical rainforests, primarily in the Amazon basin and the Guyana Plateau. It is a typical cauliflorous plant (not strictly) cross-pollinated and monoecious, and can reach up to 25 m in height in its wild state. The fruit, known as a ‘‘pod’’ is a type of indehiscent berry, varying in weight depending on the clones, and averaging around 500 g. It contains 30–60 seeds surrounded by sweet mucilage. Once fermented and dried, seeds (then known as ‘‘beans’’), constitute the fermented dried cocoa on which the chocolate industry is based.

Cocoa is usually grown under shade, after clearing the forest. Planting densities vary from 400 to 2500 (plants/ha) and average yields are between 200 and 800 kg of fermented dried cocoa per ha (Wood and Lass, 1985). The planting material, which has often undergone little improvement, is generally derived from seed. Little use is made of cuttings or budded clones, which are more difficult to grow in the early years of the plantation than seedlings. The cocoa tree is generally attacked by numerous insects and diseases: caterpillars, bugs of the mirid family, black pod rot, which is pantropical, witches’ broom and frosty pod rot in America, and Swollen-Shoot virus in Africa, etc.

Botanists distinguish between two geographical sub-species of the cocoa tree, *T. cacao* subsp. *cacao* and *T. cacao* subsp. *sphaerocarpum*, which correspond to the main two groups of historical cultivars: Criollo and Forastero (Cuatrecasas, 1964). However, breeders now prefer to consider the existence of several morpho-geographical groups, on whose hybridization genetic improvement of the plant relies (Lanaud et al., 1999). Good knowledge of the structuring of the species’ genetic diversity is therefore needed to produce high-yielding hybrid varieties. In that respect, the wild cocoa trees of French Guiana, particularly the GU accessions discovered following surveys in primary forest, prove to be original and, in most studies, irrespective of the markers, they stand out clearly from the other groups. That particularity affords them great potential interest (Lanaud, 1987; Lachenaud et al., 1999, 2004; Sounigo et al., 2001).

The main selection criteria used in cocoa tree breeding are productivity, the yield:vigour ratio (‘‘cropping efficiency’’ or ‘‘yield efficiency’’), bean size, resistance to diseases and insects, along with end-product quality. However, genetic control results remain relatively few.

The cocoa tree, like all other tropical perennial plants, still largely relies on genetic resources of wild origin being available for its genetic improvement (especially for disease resistance criteria). However, given its ecology and biology, incorporating such genetic resources into breeding programmes is a lengthy and complicated matter. In fact, wild cocoa populations are found in zones that are difficult of access (tropical rainforests of South America), which complicates surveys and the safeguarding of collected material. The length of the cocoa tree life cycle considerably lengthens breeding programmes: it takes at least 15 years between planting the first varietal trials and validating the varieties. It is also necessary to add the time imposed by compulsory quarantine between continents to avoid the spread of diseases. All that explains why several decades are often seen between the collection of genetic resources in the wild and their practical use by growers, provided those resources are not quite simply lost in the early years, during the safeguarding, characterization and assessment stages. It is thus that, nowadays, the most frequently used parents in breeding come from surveys (or selections) dating from the 1930s and 1940s. Some major surveys have taken place without the collected material being significantly used: ‘‘there are accessions that derive from collecting activities carried out 20, and perhaps 50 years ago, about which we still know little or nothing of the characteristics and utility of the genotypes represented in these collections’’ (Bartley, 2005). In that respect, surveys that were conducted in French Guiana in 1987 can be considered exemplary, given the limited loss rates observed 20 years after collection and the considerable distribution of clones in producing countries.

The International Cacao Genebank Database (ICGD, Wadsworth et al., 2003) lists 730 accessions bearing the GU prefix (clones or families of open-pollinated progenies), present in around fifteen countries. However, this number is not updated, inherent values and associated data are often few and far between, and it could be tricky making a choice for incorporating GU clones in a breeding programme. An overview of the main results acquired remains to be carried out in order to identify the potentially most worthwhile accessions: it is provided here and the best clones are indicated for the main selection criteria, along with those clones which should be avoided in breeding programmes.

2. Nomenclature and background

Up to 1989, the GU prefix (for ‘‘Guyane’’, i.e. French Guiana) was a code used at the CIRAD Paracou-Combi station (Sinnamary, French Guiana) for all the cocoa germplasm in the collection and could therefore cover quite diverse origins. Nevertheless, all the GU clones existing outside French Guiana originate from the Camopi and Tanpok river basins surveyed in 1987 (Lachenaud and Sallée, 1993). This GU germplasm only accounts for part of the wild cocoa trees of French Guiana: other accessions come from the basins of the Kérindioutou (clones with prefixes KER and B7), Oyapok (OYA, PINA), Euleupousing (ELP) and Yaloupi (YAL) rivers (Lachenaud and Sallée, 1993; Lachenaud et al., 1997).

For any GU clone, the nomenclature adopted is as follows: GU xxx–N (or GU xxx/N), where xxx is a three-figure number attributed to the original pod during the surveys, and the N suffix is a letter (exceptionally a figure) attributed to a seedling or tree derived from that pod.

During the 1987 surveys, pods were collected from 147 wild mother-trees (and two semi-wild trees), whilst two mother-trees were collected in budwood form. A pod from each mother-tree was preserved in French Guiana, the seedlings obtained were planted in a collection, and then studied individually for 10 years. Other pods, representing only 92 mother-trees, were sent to Montpellier (France) and, after quarantine, budwood taken from the seedlings obtained was sent to seven countries (Cameroon, Costa Rica, Ivory Coast, UK, Philippines, Togo and Trinidad and Tobago) between 1988 and 1990. Each seedling was given an identification suffix, defining the clone, and it was rare that two countries received the same clone. All those clones (around 500) were full-sibs (or half-sibs) of the trees studied in French Guiana; in other words, each wild mother-tree collected in 1987 should currently be represented by a family of trees, in the form of seedlings (in French Guiana) and/or clones (in French Guiana and elsewhere).

Some GU clones selected in French Guiana from 1992 onwards were delivered to the Cocoa Research Unit quarantine station in Barbados and to CIRAD in Montpellier. The quarantine stations in Reading and Barbados also delivered GU clones to other producing countries (Brazil, Malaysia, India, Indonesia, etc.). It resulted from all those exchanges that it is currently difficult to draw up a precise picture of the GU material situation, in terms of actual location of the clones, their evaluation and uses.

Our survey revealed that, in October 2006, all over the world, the number of surviving clones bearing a "GU" designation amounted to 370. In addition to those clones, mention should also be made of 145 progenies still present in the CIRAD collection in French Guiana.

3. Agronomic performance

The main agronomic results were obtained by individually monitoring 1621 trees in the "Camopi and Tanpok" collection, set up at Paracou-Combi in 1988 (Lachenaud et al., 2000; Lachenaud and Oliver, 2001). The collection comprised 144 open-pollinated progenies (families) belonging to 11 natural populations ("demes", Hartl and Clark, 1997), with an average of 11.2 trees per progeny. Each progeny came from a pod collected from a wild mother-tree and each mother-tree was only represented by a single progeny. The trees were monitored individually for 10 years, with a view to discovering family and/ or population effects for various agronomic descriptors (Table 1), including the following:

- Cumulative yield over 10 years.
- Cropping efficiency at 10 years (ratio of the cumulative yield at 10 years to the trunk cross-section, in cm^2, 50 cm from the ground).
- Losses due to rot diseases in the field (all types combined).

At the same time, some trees (ortets) were morphologically characterized for their fruits and beans, from 1994 to 2004 (Lachenaud and Oliver, 2005a; Lachenaud et al., 2006; Lachenaud, 2007), based on IPGRI recommendations (Anon., 1981). Of the agronomically useful descriptors studied, this article considers:

- The average weight of fresh beans per pod (WFB).
- Pod filling (defined by apparent fertility, AF, which is the average number of normal beans in relation to the average number of ovules per ovary).
- The average weight of one fresh bean (AW1B).

As the aim of this overview is to provide practical indications for breeders, only a selection of the set of results obtained is presented.

3.1. Production and cropping efficiency

For these two traits, which are fundamental selection criteria, and for which there existed significant "family" effects (Table 1), the best clones are presented, along with those to be avoided, by extrapolating the results from French Guiana (Table 2). The average production of the wild families was 342 kg of fermented dried cocoa per ha per year over the first seven harvests (Lachenaud et al., 2000), whereas the production of a neighbouring control plot of selected hybrids was 712 kg (Lachenaud et al., 1994). However, the yield levels were remarkable for certain wild families (equivalent to 1426 kg of fermented dried cocoa per ha per year for the first 7 years of harvests for the best family, GU 285), as was "cropping

Table 1
Significant effects (with the value of $Pr > F$ in brackets) found after 10 years of individual monitoring in the Paracou-Combi collection (French Guiana)

Criterion	"Population" effect	"Family" effect	"Individual" effect (ortet, clone)
Cumulated production	No	Yes (<0.0001)	–
Cropping efficiency	No	Yes (<0.0001)	–
Resistance to rot diseases in the field	Yes (0.0028)	–	–
WFB	Yes (0.0005)	–	Yes (<0.0001)
Flat beans (%)	Yes (<0.0001)	–	–
Pod filling	Yes (<0.0001)	–	–
Average weight of one bean	No	–	Yes (<0.0001)

Where WFB is the average weight of fresh beans per pod and (–) is the effect not tested.

Table 2
Best clones, and clones to be avoided, for the potential productivity (PP) and cropping efficiency (CE) criteria

Criterion	Best clones	Clones to be avoided
PP	GU 134-A, B, C	GU 114-F, L, P
	GU 139-A	GU 195-P, V
	GU 140-F, S	GU 221-C, H, J, V
	GU 143-A, B, C	GU 251-D, L
	GU 144-A, B, C, L	GU 261-A, P
	GU 280-A	GU 314-N
	GU 285-A, B, C	
	GU 286-A, P	
	GU 303-A, B	
	GU 325-A	
CE	GU 129-A, B	GU 114-F, L, P
	GU 134-A, B, C	GU 195-P, V
	GU 139-A	GU 251-D, L
	GU 140-F, S	GU 261-A, P
	GU 285-A, B, C	GU 314-N
	GU 286-A, P	
	GU 303-A, B	
	GU 325-A	

For PP, the best clones vary between 804 and 1426 kg of dry cocoa ha^{-1} year^{-1} for the first seven crops under the conditions at Paracou-Combi (French Guiana), and clones to be avoided are below 100 kg. For CE, the best clones vary between 0.39 and 0.50, and clones to be avoided are below 0.04 (kg of pods cm^{-2}).

efficiency'' (Lachenaud et al., 2000). For the latter criterion, the average value was 0.16 (as opposed to 0.26 in the controls), with two wild families outclassing the best control. For these two criteria, as the best populations proved to be CAM 1 and CAM 7, breeders should prefer clones derived from families GU 126 to 152, 156–161 and 250–286.

3.2. Pod filling and bean traits

For the bean traits, which are other important selection criteria, as they concern the commercial end-product used by industry, a list of clones to be preferred and avoided is given (Table 3). The best clones are those giving the highest values for WFB, AF and AW1B. The last criterion needs to be over 2.86 g, the value corresponding to the commercial limit of 1 g for the average weight of one fermented dried bean. Extrapolation of the results acquired in French Guiana to other clones has not been possible, since no ''family'' effect was directly found (Table 1). However, a significant ''family'' effect existed for the ''average weight of one pod'' (Lachenaud et al., 2000), which was positively correlated with the ''average weight of one bean'' ($R = 0.76$; Lachenaud, 2007). Table 1 reveals significant ''population'' effects for the average weight of fresh beans per pod, the flat bean rate and pod filling. Significant differences were found between ortets for the ''average weight of fresh beans per pod'' and ''average weight of one fresh bean'' descriptors (Lachenaud and Oliver, 2005a; Lachenaud, 2007). Like other Forastero germplasm, in general, GU clones have relatively small beans and poorly filled pods. However, those results, which were obtained at a single location, need to be confirmed.

Table 3
Best clones, and clones to be avoided, for bean criteria (according to data from Paracou-Combi, in French Guiana; Lachenaud and Oliver, 2005a; Lachenaud, 2007 and unpublished data)

	Best clones	Clones to be avoided
WFB	GU 285-A (124)	GU 245-A (48)
	GU 139-A (117)	GU 230-A (52)
	GU 315-A (117)	GU 303-A (54)
	GU 157-A (115)	GU 317-A (57)
	GU 252-A (112)	GU 311-A (58)
		GU 196-A (59)
		GU 182-A (59)
		GU 143-A (60)
AF	GU 238-A (0.80)	GU 303-A (0.33)
	GU 155-A (0.73)	GU 245-A (0.40)
	GU 280-A (0.73)	GU 338-A (0.42)
	GU 285-A (0.72)	GU 182-A (0.43)
	GU 270-A (0.71)	GU 317-A (0.44)
	GU 276-A (0.71)	GU 116-A (0.44)
	GU 126-A (0.71)	GU 174-A (0.44)
	GU 266-A (0.71)	GU 163-A (0.45)
AW1B	GU 315-A (3.82)	GU 311-A (2.20)
	GU 279-B (3.76)	GU 254-A (2.22)
	GU 139-A (3.58)	GU 165-A (2.37)
	GU 285-A (3.53)	GU 163-A (2.57)
	GU 157-A (3.49)	GU 344-A (2.58)
		GU 306-A (2.59)

Where WFB is the average weight of fresh beans per pod (values in brackets, in g), AF the apparent fertility (ratio of the average number of normal beans to the average number of ovules per ovary) and AW1B is the average weight of one fresh bean (in g).

3.3. Compatibility

As compatibility is sometimes considered to be an agronomic trait, it was also studied for 67 ortets, selected from nine populations (Lachenaud and Oliver, 2005b). They proved in the majority to be self-incompatible (58%) or very slightly self-compatible (34%), i.e. displaying between 15 and 25% of fruit-setting 10 days after manual self-pollination (Lachenaud and Oliver, 2005b). Those values classed them nonetheless in the ''self-incompatible'' category according to the definition by Posnette (1945), like Upper Amazon Forastero trees.

4. Resistance to diseases and insects

4.1. Resistance to black pod rot

This disease, which is the most widespread and probably the most damaging, is caused by several species of the genus *Phytophthora*, which attack fruits of all ages, leaves, branches and the trunk. The species *Phytophthora megakarya*, which is currently confined to certain African countries, seems to be the most aggressive in the field (Cilas and Despréaux, 2004).

The only data available for field losses suffered by the GU germplasm are those obtained in French Guiana, in the collection already mentioned. Only a ''population'' effect has been found (Table 1), with the population originating from the Tanpok proving to be more susceptible, whilst the Camopi populations, Cam 13, 12, 1 and 3 were less affected (Lachenaud et al., 2000). An analysis of the individual data led to the selection of 24 high-yielding ortets displaying rot resistance in the field, of which 18 were tested at CIRAD in Montpellier for their resistance to *Phytophthora palmivora* and *P. megakarya*, by early screening on leaf discs. Consequently, the main results available come from early screening in the laboratory on leaf discs (Nyassé et al., 1995; Tahi et al., 2000).

- In relation to black pod rot caused by *P. palmivora*, the results of the leaf-tests conducted mostly in Ivory Coast, Ghana and France (in the last case with very aggressive strains NS 607 and TRI 1), revealed a generally high level of resistance (Anon., 2004; Paulin et al., 2005): out of 57 clones tested, 31 (54.4%) proved to be resistant or very resistant, 17 moderately resistant (29.8%) and 6 susceptible or very susceptible (10.5%). The ambiguous cases (clones scored differently depending on the country) were rare (3, i.e. 5.3%), like the example of clone GU 255-V, which varied from susceptible (in Venezuela) to very resistant (in Ivory Coast), undoubtedly depending on the aggressiveness of the strains used (Anon., 2004).
- In relation to black pod rot caused by *P. megakarya*, the leaf tests conducted in Montpellier (Paulin et al., 2006), with a very aggressive strain (NS 269), revealed generally high resistance: out of 40 clones tested, 28 (70.0%) proved to be resistant or very resistant, and only 6 susceptible (15.0%). Seven clones were classed better than the IMC 47 control (Table 4). Only one GU clone has been tested in Cameroon, GU 255-V, where it has proved to be susceptible.

4.2. Resistance to witches' broom disease

This disease, caused by the fungus *Moniliophthora perniciosa* (previously *Crinipellis perniciosa*), is only rife in South America and on some Caribbean islands (including Trinidad). The fungus attacks pods and the tree's production potential (vegetative shoots or flower cushions). The selection of resistant planting material has to take into account those three potential targets, as their resistance to the disease is only moderately correlated (Pires et al., 1999; Thevenin et al., 2005).

In French Guiana, both *in situ* and *ex situ*, GU germplasm proves to be remarkably resistant to the local strains of the disease, to such a point that no susceptibility scoring is possible in the collection.

In Trinidad, the results on pods obtained in the field on nine clones showed that eight were resistant and one moderately resistant (Table 4). On twigs, in Ecuador and Trinidad (Anon., 2004) and in Brazil (Pires, 2003; Anon., 2004), out of 28 clones tested, 22 were resistant (78.6%), 4 susceptible (14.3%) and 2 displayed contradictory results. In greenhouse tests in Trinidad (test by spraying or using agar droplets), out of nine clones,

Table 4
Best clones (VR, very resistant and/or R, resistant) and clones to be avoided (S, susceptible; VS, very susceptible) in controlling three diseases and a group of cocoa tree pests

	Best clones	Clones to be avoided
P. palmivora (leaf test)		
Strain TRI 1	GU 123-V (VR) GU 226-V, GU 195-V GU 269-V, GU 241-V (R)	
Strain NS 607	GU 134-B, GU 254-A (R)	GU 138-A (VS) GU 230-B, GU 268-A GU 134-C, GU 301-A (S)
P. megakarya (leaf test) (strain NS 269)	GU 123-V, GU 125-C GU 195-V, GU 226-V GU 269-V (VR)	GU 129-B, GU 134-A GU 138-A, GU 265-V GU 312-V, GU 329-V (S)
M. perniciosa (in the field on twigs and/or pods)	GU 123-C, GU 125-C GU 151-F, GU 171-C GU 175-V, GU 195-P GU 219-F, GU 221-C GU 221-H, GU 241-P GU 261-P, GU 265-P GU 277-G, GU 286-P GU 300-P, GU 305-P GU 307-F, GU 307-V GU 310-P, GU 335-P GU 353-L (R)	GU 168-H, GU 259-C GU 296-H, GU 341-H (S)
Mirids	GU 183-K, GU 191-B GU 207-G, GU 207-K GU 226-R, GU 265-K GU 275-A, GU 298-B GU 322-B, GU 333-K GU 337-F, GU 343-F (VR)	GU 125-K, GU 158-G (S)

The clones for which ambiguity persists are not included.

only one (GU 255-V) proved to be susceptible (whereas it was scored resistant in the field in the three countries mentioned), five were resistant and three moderately resistant (Anon., 2003, 2004). Pires (2003) considered that the clones of the GU series were, on the whole, a new group of substantial interest, displaying resistance factors that were distinct from those of SCA 6 (or of the Trinitarios and Lower Amazons), and therefore potentially very worthwhile in crosses with those materials.

4.3. Resistance to frosty pod rot

This disease, caused by *Moniliophthora roreri*, is currently confined to certain American countries, but its recent and rapid invasion of Guatemala and Mexico, along with its current spread towards Bolivia and Brazil, make this a potentially very dangerous disease for world cocoa growing. A thick layer of white mycelium develops on the surface of the pods, containing billions of spores that can easily be disseminated by wind, water, insects or humans. A major programme to search for resistant cultivars has been under way for around 12 years in Costa Rica; however, sources of resistance to this disease are few in number and need to be enhanced.

In Costa Rica (applying a methodology described in Phillips-Mora et al., 2005), out of seven GU clones tested (W. Phillips-Mora, personal communication), four proved to be susceptible (GU 168-N, GU 200-L, GU 237-N, GU 269-H) and three ‘‘moderately susceptible’’ (GU 151-N, GU 154-L and GU 207-N).

4.4. Resistance to mirids

Mirids (often called capsids) are a group of bugs that are rife in western and central Africa, whose most harmful species (*Sahlbergella singularis* and *Distantiella theobromae*) cause damage to branches and pods, but can also kill trees. In addition, the lesions caused by mirids provide access for various fungi that can obstruct vessels (Wood and Lass, 1985; Collingwood, 1977). Some GU clones have been tested against these insects in Ivory Coast, Cameroon and Ghana.

In the CNRA collection in Ivory Coast, the scores for old and recent damage (N'guessan et al., 2007) showed the group of GU clones to be one of the most resistant groups to those insects (the most resistant for old damage and among the three most resistant for recent damage). Twelve clones showed no damage after a dozen years in the field (Table 4). In Cameroon, in budwood gardens, with artificial infestation by *S. singularis* larvae, GU 255-V, the only GU clone tested, proved to be resistant (Anon., 2004; Babin et al., 2004; Babin, personal communication). This result is confirmed in Ghana (Adu-Acheampong et al., 2007) were this clone is among 11 tolerant to mirid attacks.

5. Technological criteria

The technological criteria comprise traits such as bean size (already mentioned in Section 3.2; Table 3), chemical composition (fat content, alkaloids) and various sensory parameters, such as acidity, astringency, floral or fruity tastes, aroma intensity, aftertaste, cocoa flavour, etc. They concern the end-products used by industry and consumed.

The sensory qualities of the GU material have yet to be studied extensively, though it has been done for some populations, using fermented dried cocoa primarily produced in French Guiana (Assemat et al., 2005) and for one clone, GU 175-P, in Ecuador (Anon., 2006).

In the first work, with samples of dry cocoa produced in French Guiana and Ivory Coast, the overall aroma and ‘‘flavour’’ intensity of chocolates produced from GU germplasm has proved to be statistically better than that of the West African Amelonado which, when it comes from Ghana, is the industrial reference for those criteria (Assemat et al., 2005). The caffeine rate was also higher than that of the African Amelonado control. For the other criteria studied by Assemat et al. (2005), especially the butter rate, no significant difference was found with the controls (various Amelonados and Ecuadorian cocoas).

In the second work, clone GU 175-P, tested using fermented dried cocoa produced in Ecuador, had ‘‘a rich cocoa aroma with raisin notes’’ (Anon., 2006). Its average bean weight was 1.09 g (as opposed to 0.63 g for clone SCA 6, a reference for small beans) and its fat content was quite high (54.2%, for an average of 53.7 over the 15 samples of various morphogeographical groups of cocoa trees).

6. Value as parents

Data in Tables 2–5 concern clonal values of the GU germplasm (ortets, clones); they could be useful for choosing clones, but are particularly so for selecting parents, since the cocoa tree is primarily used in the form of inter-group hybrid varieties.

GU clones have only undergone limited testing as parents in cocoa breeding programmes, with generally quite recent trials, but the following are worth mentioning:

- In Ivory Coast (CNRA), two clones were involved in four ‘‘single pair’’ type crosses planted in 1991 (Lachenaud et al., 2001) and three (involved in 11 crosses) in a 6 × 3 incomplete factorial design at two locations in 2001, after leaf-testing of the families for resistance to *P. palmivora* (Anon., 2004). As a result of the first trial, a progeny with parent GU 133-1 (classed resistant to *P. palmivora*) has been shortlisted for multi-site confirmation trials, due to its high productivity, excellent cropping efficiency and very low losses due to rot diseases (Lachenaud et al., 2001). Some of the results acquired seem to show good transmission of resistance to *P. palmivora*: for instance, the progenies of clone GU 123-B (with parents P7, IFC 1 and IFC 11), which was classed highly resistant in the leaf test, were also classed highly resistant (Anon., 2004). In the field, the first harvests (Anon., 2006 and Tahi, personal communication) revealed an excellent performance for yield and resistance to rot diseases for hybrids with a GU parent (in this case GU 175-A, GU 123-B, GU 284-A) planted in comparative trials with other families in 2001.

Table 5
Known characteristics of GU clones in quarantine at the University of Reading (2006)

Name	Population	Production	CE	Rot in field	*Phytophthora palmivora* test	*Phytophthora megakarya* test	WB test	WB pods	WB twigs	Mirids
GU 114-P	TAN	VL	VL	S			R	MR	R-S	
GU 123-V	TAN	–	–		VR	VR				
GU 125-C	CAM 6	L	L			VR			R	
GU 133-C	CAM 7	L	L		VR					
GU 144-C	CAM 7	H	H							
GU 168-H	CAM 9	L	L						S	
GU 171-C	CAM 9	L	L						R	
GU 175-P	CAM 9	L	L		MR		R		R	
GU 183-G	CAM 9	L	L		R	R				VR
GU 195-V	CAM 9	VL	VL		R	VR				
GU 207-H	CAM 12	L	L		VR				R	
GU 219-F	CAM 3	L	L	MR			MR	R	R	
GU 221-C	CAM 3	VL	L						R	
GU 226-V	CAM 3	A	L		R	VR				
GU 241-P	CAM 3	L	L	MR				R	R	
GU 241-V	CAM 3	L	L		R	R				
GU 259-C	CAM 1	L	L						S	
GU 261-P	CAM 1	VL	VL						R	
GU 263-V	CAM 1	A	A		R	R				
GU 265-P	CAM 1	L	L						R	
GU 269-V	CAM 1	L	L		R	VR				
GU 277-G	CAM 1	H	H				R		R	VR
GU 296-H	CAM 13	L	L						S	
GU 307-F	CAM 9	L	L	S				R	R	
GU 310-P	CAM 9	L	A	S				R	R	

Where CE is the cropping efficiency, WB witches' broom, MR moderately resistant, R resistant, VR very resistant and S is susceptible. Production, in kg of dry cocoa ha^{-1} $year^{-1}$: H, high (>750); A, average (400–750); L, low (100–399); VL, very low (<100); CE, in kg of pods cm^{-2}. H, high (>0.30); A, average (0.20–0.29); L, low (0.04–0.19); VL, very low (<0.04).

- In Trinidad (CRU), in a pre-breeding programme for resistance to black pod rot, three clones have been involved in a 6 × 6 half diallel design (Ducamp, 1994), initially carried out for nursery tests, then later planted for certain families. In the nursery, 29 progenies, along with buddings of the parents, were assessed for their degree of resistance to *P. palmivora*, between 1995 and 2000, using the leaf disc inoculation method (Nyassé et al., 1995). The three Guianan clones used as parents (GU 175-P, GU 286-P and GU353-L) displayed moderate resistance levels (from 2.65 to 2.88, when symptoms were scored from 0 to 5). By crossing with clones SCA 6, IMC 67 and ICS 1, the progenies had lower resistance levels than the parental average, but not significantly so ($r = 0.65$, $pr = 0.12$). That germplasm was planted out and thereby subjected to natural black pod rot and witches' broom pressure. Three years of observations on branches were used to quantify the percentage of buds infected by *M. perniciosa* (unpublished data): clones GU 175-P and GU 286-P proved to be very resistant (0.44 and 0.00%, respectively) and GU 353-L susceptible (4.61%).
- In French Guiana (CIRAD), a genetic parameters study was conducted. Seven clones were involved in 27 crosses, in a 5 × 8 incomplete factorial trial, planted in 1997–1998. For the juvenile vigour criterion (increase in trunk section 15 cm from the ground between 1 and 2 years in the field), some unpublished results indicated that GU clones had a lower General Combining Ability than the two Upper Amazon clones tested (IMC 67 and SCA 6), but similar to that of the other clones belonging to other groups (EET 103, ICS 95 and GF 23). The Specific Combining Ability was significant and the best crosses were those involving an Upper Amazon parent and a GU parent, whilst the least good were all crosses between GU clones. Those results need to be confirmed for other agronomic criteria but, like those obtained in Ivory Coast, they seem to indicate the considerable merits of the GU group in hybridization.

Crosses involving GU clones have also been planted recently in other countries. In America, a cross of this type (GU 154-L × ICS 43) is involved in a regional trial planted between 2004 and 2006 (Costa Rica, Peru, Trinidad, Ecuador, Brazil), and in Ghana (CRIG), 14 GU clones were crossed with Upper-Amazon clones (17 crosses) and planted in 2002 (Anon., 2004).

Only a few preliminary results are available: for instance, in the Costa Rican trial, cross GU 154-L × ICS 43 is classed first (out of 13 crosses) for trunk circumference and crown height. The particular vigour of the cross is attributed to the GU parent (Anon., 2006), a particularity that seems to be confirmed in Brazil (Monteverde-Penso et al., 2005).

7. Conclusion

The GU germplasm primarily surveyed in 1987 is still well-represented 20 years after it was collected: 94% of the wild mother-trees still have representatives in collections, which is quite an exceptional result. Bartley (2005) pointed out that the

Brazilian Genetic Resources Programme had lost more than 50% of the mother-trees collected since 1976. The good results of the CIRAD programme can be partly explained by the fact that virtually only pods were taken from the mother-trees (the budding success rate is always lower) and that the material was very rapidly distributed to several countries. It currently exists in seventeen producing countries.

Twenty years after its collection in primary forests, this material is still being assessed, after largely being characterized in French Guiana, and has already been incorporated in some national breeding programmes. The results obtained on the resistance to witches' broom disease and black pod rot have revealed a high level of general resistance, which confirms the observations carried out *in situ* during the surveys and *ex situ* in Guianan collections. The group of GU clones therefore proves to be a major potential source of resistance to those diseases. The situation seems to be similar for resistance to mirid damage, but fewer results are available.

The production levels reached in French Guiana, along with the cropping efficiency, are noteworthy for some families. The best progenies have produced yields approaching 3000 kg of dry cocoa per hectare once in full production (Lachenaud et al., 2000). The first results obtained in Ivory Coast showed that GU clones seem to reveal a high heterosis effect for yield in hybridization with other widely used groups.

Bean-related criteria have shown that, in general, GU clones have relatively small beans and poorly filled pods, which are common defects of Forastero cocoa trees. However, there exists substantial variability and some worthwhile clones can be selected and recommended. The sensory value, about which little is known yet, seems nonetheless interesting, with a strong cocoa flavour.

This overview, along with the results already published on the spatial structuring of the genetic diversity found in GU material (Lachenaud et al., 2004), should therefore provide breeders with a relatively easy choice of parents to be incorporated into their breeding programmes. GU clones also possess the interesting property of being virtually homozygous, with 6–11% heterozygosity being observed with biochemical markers (Lachenaud et al., 2004).

For the whole set of criteria – yield, cropping efficiency, bean size, average weight of fresh beans per pod, apparent fertility, resistance to rot diseases in the field confirmed by the leaf test – three clones selected in French Guiana and characterized can be recommended: GU 285-A, GU 134-B and GU 139-A. These three clones, used as parents in breeding programmes, could provide significant genetic progress. In addition, some clones in quarantine in Reading (UK), and therefore available and easily accessible, display worthwhile resistance capacities (Table 5). Five of them are also included in the CFC/ICCO/IPGRI collection (Sounigo et al., 2007): among them, GU 175-P, GU 241-P and GU 261-P are resistant to witches' broom disease and, in the first two cases, display a degree of resistance to *P. palmivora*. GU 133-C (and in most cases GU 255-V) displays high resistance to *P. palmivora*.

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