



# Study of the genetic diversity of cocoa populations (*Theobroma cacao* L.) of Martinique (FWI) and potential for processing and the cocoa industry

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**Abstract** The establishment of cocoa (*Theobroma cacao* L.) in Martinique is an old story. Some authors believe that the first cocoa trees were planted there by the native Caribbean people, while others indicate that cocoa was introduced in the seventeenth century. Since then, the history of cocoa farming in Martinique has been punctuated by different waves of introduction from various countries and by cyclonic episodes that ravaged its cultivation. Today, there are many cocoa trees coming from this turbulent history and this

current study has started to better understand the genetic diversity of the current orchards. Our interest in Martiniquan cocoa also comes from very encouraging results on aromatic properties of chocolates made with Martiniquan beans. A total of 161 cocoa trees located from the different regions of the island were genotyped, using a set of SNP markers. Sensory descriptive profiles of the chocolates coming from these trees were carried out by a provider laboratory, according to the sensory method described by AFNOR

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(French Agency for Standardization) NF ISO 11035 (July 1995). We observed a genetic diversity within the Martiniquan cocoa orchards with a genetic admixture consisting of ancestry of 6 out of the 10 *Theobroma cacao* ancestral genetic groups which testifies to these numerous waves of introduction; the main representative ancestry group is Amelonado, then Criollo. The first tests of sensory analysis revealed a strong aromatic potential of Martiniquan cocoa, probably due to a favorable terroir effect.

**Keywords** *Theobroma cacao* L · Genetic diversity · Terroir · Martinique (FWI) · Sensory profile · Fine chocolate

## Introduction

The history of cocoa in Martinique is very old. Several seventeenth century writers, who lived in Martinique, testified to the presence of cocoa trees on the island around 1660, and attributed their discovery to the Amerindians (Banbuck 1935; May 1930; Nicolas 1996). In 1667, Father Du Tertre reported «Native people showed M. Du Parquet, in 1655, this treasure which was hidden in Capesterre; fortunately several people have planted it and cultivate it now» (Du Tertre 1667). In 1660, a report from the priest Tuscan Cosimo Brunetti, who lived 8 months in the West Indies and especially in Martinique from September 1659 to April 1660, also indicated the presence of cocoa trees (Ouellet 2014). However, the location of the first cocoa plantations and the identity of their first owners in Martinique are the subject of disagreement. Generally, the authors favor the hypothesis followed recently by historian Jean-Pierre Sainton (2004) and by biologist Basil Bartley (2005), who both affirmed that the first cocoa estate of Martinique dated from 1660, and that it would have been created between Morne-Rouge and Saint-Pierre by Sieur Benjamin d'Acosta, a Portuguese expelled from Brazil. Bartley's assumption was grounded on a nineteenth century book by Guérin (1896) dealing mainly with Guadeloupe but relying also on father Labat (1724), without specifying which edition of Father Labat's book he used. Sainton gave no precise reference, but seemed to rely on Leo Elisabeth, who did not cite his sources either. Thus both positions are not extremely strong.

The situation is even more complex since there have been many editions of Father Labat' book and not all of them are identical. For instance, the 1724 edition of the *Nouveau Voyage aux isles de l'Amérique* by Jean-Baptiste Labat, contained a contradictory piece of information concerning the role of Benjamin d'Acosta. In Volume 2, father Labat asserted that Benjamin d'Acosta was the first creator of a cocoa orchard, whereas, in volume 2, he indicated that his estate was not the first cocoa farm, but one among the first cocoa farms in Martinique. Therefore it seems impossible to conclude without some more archival work. Failing that, we can stick to the dominant position, taking into account the fact that it was shared by the contemporaries as early as the beginning of the eighteenth century and especially by father Labat in 1724 and Quelus in 1717.

Since then, the history of cocoa farming in Martinique has been punctuated by different waves of introduction from various countries, and destruction due to extreme climatic events like hurricanes.

According to Elisabeth (2003), cocoa cultivation was mainly developed in the early eighteenth century. In 1715, only 1900 cocoa trees were already planted on about 13 hectares compared to 13,500,000 trees in 1726 on 9000 hectares (Sainton 2004). This quantity is generally regarded as the peak of cocoa production in Martinique and the main production area was then located around Gros-Morne. However, the general census of Martinique in 1727 offered even more significant results with 17,492,950 feet of cocoa, the vast majority of which located in the Trinité district (National Archives). From the nineteenth to the twentieth century, cyclonic, seismic and disease events strongly impacted cocoa cultivation in Martinique. In the nineteenth century, cocoa remained cultivated in all the municipalities of the island. Then in the 1920s and 1930s, competition from African countries and constraints from the world market led to a decline in cocoa production; the production was around 500 t per year (Burle 1962). Around the Second World War, production fell again. In 1940, Martinique produced around 250 t of cocoa (compared to 150 t of coffee and 642,700 t of sugar). In 1943, production fell to 200 t and 130 t of coffee. The production was gradually abandoned in favor of other crops such as sugarcane, pineapple and banana. With less than 5 t of merchantable cocoa delivered in 2012, at the only

chocolate factory in Martinique, production is now anecdotal.

In its peak production period, the cocoa from Martinique enjoyed an international reputation. National Archives documentation mentioned the direct export of cocoa from Martinique to Cadix in Spain and to Saint-Thomas Island at the end of 1690ies but also to the French part of Saint-Domingue at the end of the eighteenth century. However, in Bordeaux, at the end of the eighteenth century, cocoa from French Saint Domingue or Martinique remained less highly rated than the Caraque variety from Venezuela. On this basis and in line with the evolution of the international market for label of excellence, the Pôle Agro Ressources et de Recherche de Martinique (PARM) was set up in 2012, in conjunction with the socio-economic factors of Martinique, as a research, development and support program for producers to revive cocoa production in Martinique. Around twenty producers then committed themselves by means of a charter to rehabilitate their cocoa farms, acquire good cultural practices and post-harvest treatment to obtain a cocoa of excellence. Today, these producers are structured in the VALCACO Association, which is committed to building and sustaining this cocoa sector of excellence.

Under this support program, the inventory carried out in 2012–2013 revealed a good sanitary situation of the cocoa trees of Martinique, despite the presence of several diseases in the rest of the Caribbean islands (*Phytophthora* pod rot, witches broom and frosty pod rot) and cocoa trees often more than 75 years old. This inventory has also revealed a great diversity of shape, size and color of pods, with nevertheless phenotypic traits close to those of the Amelonado genetic group. However, the phenotypic diversity of pods is not enough to reveal the genetic diversity of cocoa trees. Therefore, Single Nucleotide Polymorphism (SNPs) molecular markers through the development of Genotyping by Sequencing (GBS) libraries were used to decipher precisely the genetic diversity of cocoa trees currently present in Martinique. Compared to other genotyping methods, GBS is a high-throughput, low-cost technology, which is useful for large-scale SNP discovery and highly informative for ancestry assignments in *Theobroma cacao* (Osorio-Guarín 2018). In order to support the economic development of the cocoa sector and preserve this heritage culture, it became important to know precisely the genetic

diversity of cocoa trees in Martinique and to highlight their potential. The objective was also to identify and propagate the most interesting genotypes from a sensory quality point of view.

The aims of the study were i) to analyze the genetic ancestry and admixture of the population of Martinique ii) to map the current population in order to allow localization and preservation of individuals and iii) to know the potential of cocoa from Martinique for processing and its potential use by the chocolate industry.

## Materials and methods

### Cocoa trees sampling

An inventory of the cocoa farms of Martinique was done previously, in connection with the Martinique Chamber of Agriculture, the Martinique Regional Nature Park and the VALCACO Association. Cocoa leaf samples were collected throughout the territory at the level of old cocoa farms, active cocoa farms, as well as isolated trees (Fig. 1). The GPS coordinates of each sampled cocoa tree were recorded for tree identification and subsequent mapping. Each tree sampled was also physically marked.

### Sampling and conditioning of leaves

Two sampling campaigns were conducted at one year intervals: May, June and October 2014 (94 trees); October 2015 (67 trees); with a total of 161 samples. On a sampled tree, coming from seed (no grafting), at least three leaves were sampled and used for DNA analysis. The leaves were vacuum packed in plastic bags, before shipment for DNA extraction.

### DNA extraction, GBS library preparation and sequencing

Total genomic DNA from leaf samples was extracted as described by Risterucci et al. 2000. Sample GBS libraries were constructed as described by Elshire et al. (2011). A double digest reaction PstI/MseI was applied to 200 ng genomic DNA and followed by ligation with a barcode adapter and a common Illumina sequencing adapter. Amplified multiplexed libraries were purified and verified by fragment size



**Fig. 1** Map of the leaf sampling done from cacao trees in Martinique, in different areas (North Atlantic, North Caribbean, Centre, South)—May, June, October 2014 (94 trees sampled) and October 2015 (67 trees sampled)

analysis using Bioanalyzer High Sensitivity DNA chips to ensure that most of the DNA fragments were between 150 and 300 bp.

Libraries were sequenced on Illumina HiSeq 2500 system (150 bp, single-end reads) at the Genome and Transcriptome platform of Genotoul, France.

#### SNP calling

Sequencing fragments were analyzed using Tassel 5 GBS v2.2.24 pipeline (Glaubitz et al. 2014) and parameter (-mnQS 20). Reads were aligned to the Criollo B97-61/B2 genome version 2 (Argout et al. 2017) using Bowtie2 (end-to-end algorithm) and in -very-sensitive mode. Reads that aligned at different

locations of the genome were discarded. SNPs were called and variant call data were filtered out with VCF tools (Danecek et al. 2011). First, indels and non-biallelic sites were excluded. Then, genotyped data with less than 10 reads were recoded as missing data. Individuals with more than 50% of missing data were discarded and SNPs with more than 10% of missing data were excluded. Finally SNPs with minor allele frequency  $> 0.05$  and with a minimum distance of 64 bp were selected for further analysis.

#### Population diversity and ancestry analysis

The genetic admixture of the Martinique population was evaluated using a set of SNP markers. Individual ancestral estimates were calculated using the software Admixture v1.3.0 (Alexander et al. 2009), with supervised admixture analysis performed using 30 reference individuals with  $> 0.85$  proportion ancestry within the 10 *T. cacao* ancestral genetic groups defined by Motamayor et al. (2008). The geographic distribution and density plots of ancestry were computed using R and package ggmap and ggplot2.

#### Sensory analysis

Sensory descriptive profiles were carried out by a provider laboratory, according to the sensory method described by AFNOR (French Agency for Standardization) NF ISO 11035-Research and Selection of Descriptors for the Development of Sensory Profiles. The products (70% cocoa dark chocolate) were evaluated by an expert jury of 8–15 people, trained to identify and characterize the sensory criteria of chocolates. The tasting session consisted of a sample repetition, a random and anonymous sample distribution.

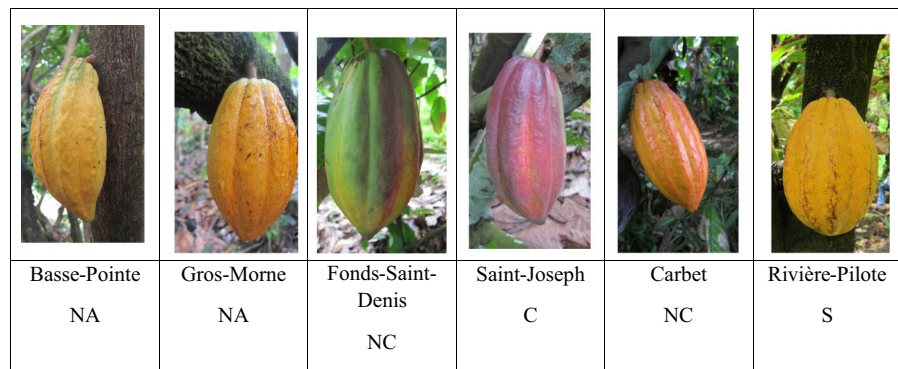
A total of 14 chocolate samples was tasted according to the sampling plan below (Table 1):

- 10 samples of chocolates made from the VALCACO producers' harvest, corresponding to known production areas,
- 2 chocolate samples made from merchantable cocoa from international trade were also tested as controls,
- 1 sample of chocolate made by a chocolate maker in Martinique, corresponding to a mixture of different production areas in Martinique, from harvests made by farmers.

**Table 1** List of 70% dark chocolate samples for the sensory analysis taking into account their production zones

N° Lots Martinique	Production zones	Geographic location
1	LORRAIN	North Atlantic
4	VAUCLIN	South
5	FRANCOIS	South
6	SAINT-JOSEPH	Centre
7	CARBET	North Caribbean
10	LAMENTIN	Centre
11	RIVIERE-SALEE	South
12	CARBET	North Caribbean
13	PRECHEUR	North Caribbean
14/15	CARBET	North Caribbean
17	RIVIERE-PILOTE	South
N° control lots	Production zones	
2	Colombia	
3	Madagascar	
16	Martinique (Bulk)	

**Fig. 2** Pods diversity—  
NA: North Atlantic; NC:  
North Caribbean; C: Centre;  
S: South



The descriptive characterization included 21 taste descriptors. This characterization was based on a qualitative and quantitative evaluation. An 11-point scale between 0 and 10 (absent to very pronounced) makes it possible to note the intensity of the different sensory criteria.

The statistical processing tools used by the provider laboratory for the evaluation of the results are the analysis of variance and the Hierarchical Ascending Classification (HAC).

## Results

### Martinique population sampling

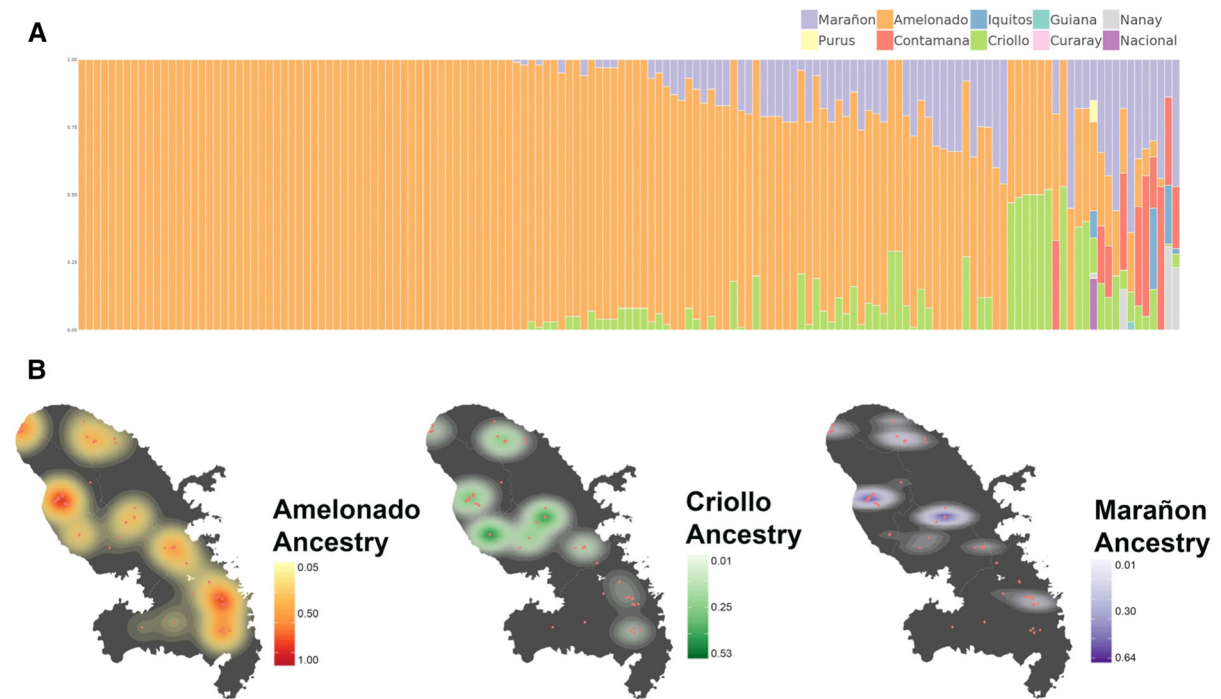
The cocoa leaf samples were taken from 161 individuals, taking into account the distribution of the agricultural/soil/climatic zones found in region (North Atlantic—NA; North Caribbean—NC; Centre—C; South—S). The distribution of the number of individuals sampled was 19.73% for NA, 25.85% for NC, 20.41% for C and 34.01% for S. The location of the sampling zone is given in Fig. 1.

The observations of morphotypes have been made on some trees, as there were pods available, thereby providing evidence of the following different morphotypes (Fig. 2): (1) Yellow-orange pods at maturity, small size, ovoid with deep grooves, (2) Yellow-orange pods at maturity, small size, ovoid with a pointed end, (3) Yellow-green pod at maturity, bigger size, rounded, smooth, (4) Yellow-green pod, medium size, large grooves and rounded, (5) Yellow-red pod at maturity, large size, elongated with deep grooves and a pointed end, (6) Violet-red pod at maturity, large size, elongated, large grooves.

### Genotype calling, genetic diversity and structure analysis

The 161 individuals from Martinique were sequenced in 2 lanes of a HiSeq 2500 (96plex) according to the method described in Materials and methods. The tassel GBS pipeline was applied for genotype calling, generating 119 537 Single Nucleotide Polymorphism (SNP) raw molecular markers. After filtering (see methods), 14 samples from Martinique were discarded and 147 individuals from Martinique and 4 113 SNP markers were selected for further analysis. In parallel, 30 reference individuals with > 0.85 proportion ancestry within the 10 *T. cacao* ancestral genetic groups where genotyped with the same SNP markers dataset.

Proportion of ancestry relative to the 10 genetic groups described by Motamayor et al. (2008) for the Martinique population is given in Fig. 3a. This analysis revealed that the Martiniquan population was preferentially from Amelonado ancestry with an average proportion ancestry across individuals of 0.80 followed by Maraño (0.10) and Criollo (0.06). A total of 80 genotypes had Amelonado ancestry  $\geq 0.85$  representing 54% of the Martinique population and 57 genotypes had 100% ancestry with Amelonado genetic group. Genotypes with Maraño, Contamana, Iquitos, Criollo or Nanay ancestry  $\geq 0.20$  were identified for 35, 8, 2, 15 and 2 genotypes respectively. Within the Criollo ancestry group, 8 genotypes have Criollo ancestry  $\geq 0.40$ . Genotype (FDOF-01-150514) differed from other individuals by having a large part of ancestry (52%) from the Contamana genetic group. Furthermore, 2 genotypes also differed from other individuals of the Martinique population by the fact that they did not have Amelonado ancestry in their genetic profiles.



**Fig. 3** Martiniquan cocoa genetic diversity. **A** Proportion of ancestry relative to the 10 genetic groups described by Motamayor et al. (2008). **B** Density plot showing the

geographical distribution of ancestry of the 3 main genetic groups. *Red points* indicate individual locations

The distribution of individuals and their ancestry estimates for the 3 main ancestry groups (Amelonado, Criollo, Maraño) are presented in Fig. 3b. In addition to variation between individuals, we observed geographical differences in ancestry. The proportion of Amelonado ancestry seemed to be well distributed across the whole Martinique island and individuals with Amelonado ancestry  $> 0.8$  were found both in south and north regions of Martinique. The situation for Criollo and Maraño ancestry seemed to be different. Criollo and Maraño ancestry were found to be higher in north Martinique than south Martinique. Individuals with highest Criollo ancestry ( $> 0.4$ ) were found to be located in Saint Joseph, Case Pilote and Fond Saint Denis production areas while individuals with highest Maraño ancestry were located in Saint Joseph, Fond Saint Denis, Le Carbet and Basse Pointe production areas.

### Sensory analysis

The results presented hereafter are extracts from the analysis report of the laboratory services provider

selected to conduct the sensory characterisation sessions on the 13 chocolate lots.

The analysis of sensory criteria showed significant differences between the samples. For the basic tastes: (1) Acidity is present in chocolates number 11, 14/15, hardly present in lots number 4 and number 10, ((2) Bitterness is present in chocolate number 16, hardly present in lots number 2, 4, and 5, (3) Sweetness is present in lot number 10 and hardly present in chocolate number 6 and 16, 4) Astringency is present in lot number 10 and hardly present in chocolates number 6 and 16.

For aromas and qualitative description: (1) chocolate note was weakly detected in chocolate number 16, (2) the criterion delicate is pronounced in lots number 7 and 10 and hardly present in lot 16, (3) dried fruits aroma (hazelnut, almond, walnuts) are distinct in chocolates 6 and 16, but hardly so in sample number 1, (4) dried fruit aroma (apricot, date, fig) are weakly present in chocolate number 16, (5) red fruit notes (raspberry, strawberry, cherry) are present in lot number 3 and 6, (6) exotic fruit aromas are somewhat separate in chocolate number 16, (7) spicy aromas are

**Table 2** Ascendant hierarchical classification for the criteria « aromas » and « descriptive quality »

Group	1	2	3	4	5	6
Product code	1	2 11 14/ 15 17	3	4 5 7 10 12 13	5	6 16

present in lot number 16 and hardly present in lot number 3, (8) alcoholic aroma (lightly fermented red fruit) is present in chocolates 1 and 6, (9) a woody note is distinct in lot number 6, (10) animal and grassy notes are significantly present in chocolate number 16 with an average quality note significantly weaker and different from the other chocolates.

The HAC analysis of the data «Aromas» and «descriptive quality» allows separation of the chocolates into 6 classes (Table 2):

Class 1: a chocolate (No.1) with less pronounced dried fruit aromas, spicy aromas, an alcoholic note linked to fresh fruit aromas.

Class 2: 4 chocolates (No.2, 11, 14/15 and 17) with chocolatey and exotic fruit aromas.

Class 3: a chocolate No.3 characterised by yellow fruit, red fruit, dried fruit and earthy notes.

Class 4: 6 chocolates (4, 5, 7, 10, 12, 13) with chocolatey, soft, spicy and dried fruit aromas.

Class 5: chocolate 6 with notes of spice, woody, dried fruit, floral, citrus, red fruit and alcoholic; an aromatic and complex chocolate.

Class 6: a chocolate No.16 characterised by the presence of animal, grassy, spicy, earthy, cocoa, dried fruit notes and an inferior quality compared to the other chocolates.

In summary, the descriptive profiles established by the mean values obtained for each product and for each descriptor allow the identification of specific aromatics (faults or strengths). Generally, the chocolates overall have a relatively weak acidity and bitterness (less than 5). The sweet note is detected (weak intensity) without being too strong. The chocolate aroma is identified for all the samples, except for the lot No. 16 for which the cocoa note is greater than the chocolate note.

The descriptive quality is satisfactory for all the chocolates, except for the lot No. 16, whose quality is reduced by negative factors (grassy, mould, green...). The chocolate coming from production zones associated with the VALCACO producers possesses some sensory characteristics of fine cacao types—and shares the same status as sample No. 2 from Colombia (Table 3).

**Table 3** Results of the sensory profiles determined for 14 samples of 70% dark chocolate

Product Code	Score/10	Notes of red fruit	Notes of yellow fruit	Notes of dried fruits	Notes of citrus	Soft	Notes of spices	Floral	Fine quality cocoa
1	6,00						×		×
2	6,42	×					×	×	×
3	6,5	×	×						Undergrowth note, moldy note detected
4	6,42							×	×
5	5,92			×		×			×
6	6,83	×		×		×	×	×	×
7	6,50		×			×	×		×
10	6,92		×			×	×	×	×
11	6,75					×	×	×	×
12	6,17			×			×		×
13	6,50		×		×		×		×
14/15	6,83	×			×				×
16	5,17								Vegetal, under fermented
17	6,42				×		×		×

The control batch No. 16 coming from harvest conducted by private individuals in different zones of the territory do not have sensory characteristics of fine cacao, along with lot No. 3, coming from Madagascar. The mastery of harvest and post-harvest treatments by the private individuals is a critical point for the lots coming from these harvests.

## Discussion

The genetic analysis revealed the genetic admixture of cocoa trees collected in Martinique. Ancestry of 6 out of the 10 ancestral genetic groups was found in the population: Amelonado, Marañon, Contamana, Nanay, Iquitos and Criollo. This large diversity has led to the appearance of, to date, undescribed hybrids, bearing the uniqueness of the region and very favourable organoleptic qualities. However, the two main representative groups were Amelonado and Criollo, coming from old introductions. These results are consistent with varieties described by Guérin en 1896, who indicate that principal variety, presumably descended from the introduction attributed to Da Costa, was called Créole and this variety form the bulk of the cocoa on Martinique (Bartley 2005). This author also relates than a later report on the situation in Martinique stated that Criollo could be found on the island (Bartley 2005). This great genetic diversity testifies to the different waves of introduction of cocoa trees on the island, as was the case in the Dominican Republic (Boza et al. 2013). The geographical distribution of the genotypes is due to human activities and not due to the structure of the landscape like for native species (Murray et al. 2019).

With respect to the historical facts described in the literature, we are not privy to exact information on the cocoa varieties cultivated in Martinique in the seventeenth century. Nevertheless, a treatise from the beginning of the eighteenth century reports on the local use of mixing by half the variety from our islands with that of the “coast of Caracas” (Caracas, Venezuela) which is smoother and less bitter (Quélus 1717). The author also specifies that cocoa from the Caracas coast is “a little flat, quite resembles by its volume and shape to one of our big beans’ and that the bean ‘of St Domingue, Jamaica and Cuba is bigger than that from Martinique”.

According to Françoise Hatzenberger (2001), the cultivated variety in Martinique in 1727 is originally

from the Lower Amazon basin, recognizable by its elongated pods and its red or green ribs (ridges) at maturity with a very accentuated tip at its lower end and its fresh white cotyledons. In 1767, the revival was guaranteed by the locals with partial use of a variety originating from Venezuela, from the Orinoco basin: an Amazonian Forastero *T. cacao*.

These historical elements described in the seventeenth and eighteenth centuries can explain the genetic diversity of the cacao trees found in Martinique. The different flows of genetic material from Central America to the Caribbean, from Trinidad to the French Antilles and also between Caribbean islands also corroborate the results found. This genetic diversity is present in all of the northern and southern Martinique regions, with however, a predominance of individuals of Amelonado ancestry in the south.

With respect to the value of this information for the transformation of the cocoa industry, the sensory characterisation results have demonstrated some sensory characteristics of fine quality cocoa, of the same degree as other merchantable cocoa found on the international market. Apart from the genetic effects on quality, environmental effects, also influence cocoa quality (Niether et al. 2017), as found for coffee (Decazy et al. 2003). In the case of cocoa, the environmental effect includes also the microbiological composition during the fermentation process (Schwan and Wheals, 2004). The genetic results obtained for the cocoa trees, some which are more than 75 years old, are in agreement with the writings of priest Toscan Cosimo Brunetti, in 1660: “there are in the forests in Capesterre, in the eastern part of the island conserved by the Amerindians until their expulsion in 1658, a quantity of cocoa, which being the best species for making chocolate would be of tremendous gain if we would apply ourselves to its cultivation and multiplication for the purpose of trading”.

The cocoa sector is developing with the desire to develop a sector of excellence in Martinique. To achieve this goal, several actions are underway: (1) creation of a Martinique cocoa collection for the conservation of this genetic diversity, (2) increased cultivated area in order to respond to the sourcing needs of the processors and valuation of the transformation into fine chocolate, (3) implementation of a distinctive quality mark or label for the international recognition of Martinique’s cocoa.

In light of these activities, it is expected that the information furnished by this work will provide key baseline data that will suitably guide industry decisions.

In order to continue this work, the study of phenotypic and morphological variations of these accessions will be initiated. The aim will be to compare Martinique cocoa trees with those found in the Caribbean, especially those of the International Cocoa Genebank of Trinidad and Tobago (Bekele et al. 2006).

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