Banana

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The world production of banana was estimated at 84 million tonnes in 1996. It has the largest production in the world among fruits and the largest international trade, greater than apple, orange, grape, and melon. Banana is cultivated in more than 120 tropical and subtropical countries across five continents. Banana production is important in terms of food, society, and economy, as well as the environment.

There are two major channels of production: bananas cultivated for export and bananas reserved for local markets.

The bananas cultivated for export, known as Grande Naine, Poyo and Williams, belong to the subgroup of triploid bananas of the Cavendish type. They differ from each other only in somatic mutations such as plant height and conformation of regimes and fruits. Their production relies on an intensive monoculture of the agro-industrial type, with no rotation, and a large number of inputs.

The cultivation of bananas for local consumption is based on a large number of cultivars adapted to different conditions of production as well as the varied uses and tastes of consumers. The production systems of these bananas generally use little or no input.

Diploid bananas, close to the ancestral wild forms, are still cultivated in Southeast Asia. In other regions, triploid cultivars belonging to different subgroups—Plantain, Silk, Lujugira, Gros Michel, Pisang Awak—are the most widely distributed.

Bananas have many uses. They are consumed as fresh fruits but also cooked, as with Plantains. They are processed in various ways, into chips, fries, fritters, purees, jams, ketchup, and alcohol (banana wine and beer, production of which is particularly high in East Africa). The daily per capita consumption of bananas varies from 30 g to over 500 g in some East African countries. Apart from the fruit, other parts of the plant are used: the pseudostem is used for its fibres and as floaters (*M. textilis* or abacca) in the Philippines, and the leaves are used to make shelters or roofs, or as wraps

for cooking (Plantain in Africa). In Thailand, the floral buds of particular varieties (Pisang Awak) are used in various culinary preparations. Finally, some varieties are considered to have medicinal properties.

Cultivated throughout the world, bananas are threatened by several diseases and pests. The greatest constraints are exerted by the nematodes—*Radopholus similis* and several representatives of the genus *Pratylenchus*—and by the black weevil of banana, *Cosmopolites sordidus*. Various fungal diseases are also major constraints in industrial production and, to a lesser degree, in local production. For example, yellow sigatoka due to *Mycosphaerella musicola* and black leaf streak disease caused by *M. fijiensis* result in harvest losses in large industrial plantations and necessitate costly pest treatment. In certain production zones, Panama disease due to the soil fungus *Fusarium oxysporum* f. sp. *cubense* prevents the cultivation of varieties of the Gros Michel type. Finally, viral diseases are spreading, or perhaps are simply better detected. Those of greatest concern are due to CMV (cucumber mosaic virus), BSV (banana streak virus), BBTV (banana bunchy top virus), and BBMV (banana bract mosaic virus).

BOTANY AND TAXONOMY

Botany

Bananas are monocotyledons originating from Southeast Asia and belong to the genus *Musa*, of the family Musaceae, order Zingiberales. The banana is a giant plant with a pseudostem formed by the interlocking of leaf limbs and measuring from 1 to 8 m. The leaves emerge from the terminal meristem of the true stem, incorrectly called the bulb, which is underground and small. The bud located at the leaf axil of each leaf may develop as a shoot. At the end of the vegetative phase, the change in the function of the central meristem induces the growth and elongation of the true stem at the heart of the pseudostem, then the emergence of the inflorescence. The inflorescence, which can be vertical, pendant, or subhorizontal, forms a cluster. It is made up of imbricate spathes arranged in a helix, at the axils of which emerge simple or double rows of flowers.

The flowers of the first rows are female (developed ovary, presence of stamenoids) or in some rare cases hermaphrodite (developed ovary and stamens). The cavity of the inferior ovaries may be filled with seeds and pulp to form the fruit. These rows of flowers, or 'hands', form the bunch. After the female hands, the hands of neutral flowers appear (neither male nor female), then the hands of male flowers (reduced ovary, well-developed stamens). In some cultivars, the growth of the apical meristem is interrupted after the appearance of female hands, but in general the inflorescence grows indefinitely to form what is incorrectly called the male bud.

Wild bananas have fruits filled with seeds and containing little pulp. Cultivated bananas, on the other hand, are of the true parthenocarpic type. The cavity of the inferior ovaries is filled with pulp to form the fruit, without pollination or formation of zygote. Most of these bananas have high, nearly total, female sterility and usually have no seeds in their fruits. For all bananas, the perenniality of the plant is ensured by natural vegetative propagation by new shoot formation; each variety is thus a clone.

Basis of Classification

The genus *Musa* comprises four sections: *Australimusa* (2n = 20), *Callimusa* (2n = 20), *Rhodochlamys* (2n = 22), and *Eumusa* (2n = 22). In this last section are found almost all of the cultivated bananas with the exception of Fe'i, diploid cultivated bananas of the Pacific region belonging to the *Australimusa*. The *Callimusa* and *Rhodochlamys* essentially contain species of floral interest.

Morphotaxonomy has enabled us to characterize the varieties of bananas and draw up a basis for the botanical classification used at present. In 1865, Kurz proposed the hypothesis of a bispecific origin of cultivars—*Musa acuminata* and *M. balbisiana* (Fig. 1). Simmonds and Shepherd (1955), using a method of scores, specified the relative contribution of two species of origin in the constitution of cultivars. Among the numerous morphological characters from which we can characterize a banana, these authors have retained 15, chosen for their stability and capacity to discriminate among the different groups of cultivated bananas. Each character has been quantified on a scale of 1 to 5, in which 1 corresponds to a phenotypic expression of wild bananas of the species *M. acuminata*, called A, and 5 corresponds to that of wild bananas of the species *M. balbisiana*, called B. For each cultivar, the level of ploidy and the score obtained by the addition of notes for each of the 15 characters determine its genomic constitution and consequently its position in a given group (Table 1). The majority of cultivars are categorized in the groups AA, AAA, AAB, and ABB.

Within each genomic group, cultivars that have a high proportion of common morphotaxonomic characters and are derived from one another by mutations are grouped together into subgroups (Table 2).

Information provided by molecular markers has demonstrated the marginal implication of *M. schizocarpa* (genome S, section *Eumusa*) and *M. textilis* (genome T, *Australimusa*, 2n = 2x = 20) in the genomic constitution of some cultivars, which are classified as AS, AT, or AAT.

Sexual Reproduction and Interfertility

Wild bananas reproduce sexually as well as by vegetative propagation. Some species, such as *M. schizocarpa* and *M. acuminata* ssp. *banksii*, are preferentially autogamous, the first flower hands of the inflorescence being hermaphrodites.

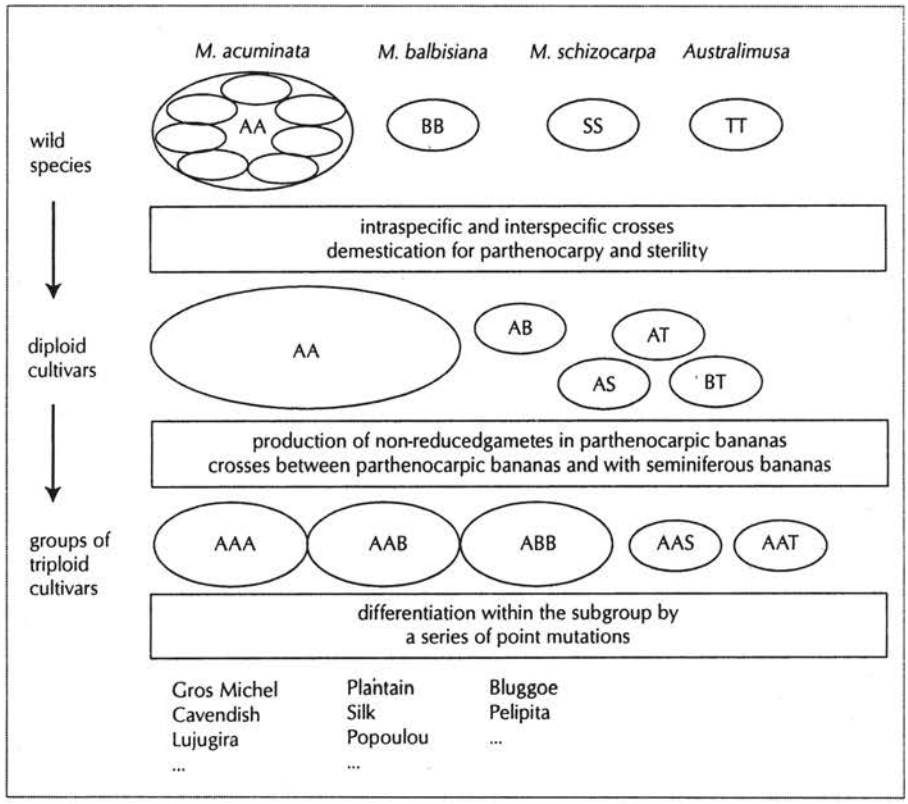

Fig. 1. Domestication of bananas

In the other species, the basal flowers are female and the banana plants allogamous. Nevertheless, these species often cross in bunches, which enables self-pollination by interposed shoots (geitonogamy).

In Asia, where the seminiferous forms are always present, some hybrids between the sections have been identified, between *M. acuminata (Eumusa)* and *M. laterita (Rhodochlamys)* and between *M. balbisiana (Eumusa)* and *M. textilis (Australimusa)*. Several interspecific hybrids, AB and AS, have also been found.

The species *M. acuminata* has a wide diversity of forms. It has been organized into interfertile subspecies on the basis of morphological characteristics and geographic distribution. Moreover, from cytological observations, Shepherd (1987) established a nomenclature of this species in seven groups within each of which the clones are structurally homozygous. The hybrids between these groups are heterozygous for one to four translocations or inversions, which limit the introgressions. These groups for the most part confirm the organization into subspecies.

Table 1. Deduction of the genomic constitution of a variety from information on its level of ploidy and its score. The intervals of scores are indicated in parentheses (Simmonds and Shepherd, 1955)

Theoretical score	Level of ploidy		
	2x	3x	4x
15	AA (16-23)	AAA (15-21)	AAAA (15-20)
30			AAAB (27-35)
35		AAB (26-46)	
45	AB (46-49)		AABB (45-48)
55		ABB (59-63)	
60			ABBB (63-67)
75	BB	BBB	BBBB

Table 2. The different types of cultivated triploid bananas

Genomic group	Subgroup	Type*	Present geographic distribution
AAA	Gros Michel**	dessert	world, regions
	Cavendish**	dessert	industrial production
	Red/Green Red	dessert	Pacific, Antilles, Philippines
	Lujugira-Mutika	cooking, beer	East Africa
	Ibota	dessert	Thailand, Central Africa
AAB	Silk	dessert	Far East, Latin America, Caribbean
	Pome-Prata	dessert	India, Australia, Hawaii, Brazil, Africa
	Mysore	dessert	India, Brazil
	Pisang Kelat	mixed	India, Malaysia
	Pisang Rajah	mixed	Malaysia, Indonesia
	Plantain**	cooking	Philippines, Latin America, Central and West Africa, Caribbean
	Popoulou-Maia Maoli	cooking	Pacific
	Laknao	cooking	Philippines
	Iholena	cooking	Pacific
ABB	Bluggoe**	cooking	Philippines, Pacific, Latin America, Caribbean, East Africa
	Monthan	cooking	India
	Pelipita	cooking	South America
	Pisang Awak	dessert	India
	Peyan	cooking	India
	Saba	cooking	Philippines

*The dessert or cooking quality of a fruit is highly subjective; most of the dessert types can also be consumed cooked, but the reverse is only rarely true.
**The most widespread subgroups.

Cultivated bananas are highly sterile. Several phenomena causing meiotic abnormalities lead to gametic sterility. These phenomena may be genomic (Bakry et al., 1990) (partial homology of two genomes *acuminata* and *balbisiana*), related to chromosomal structure (such clones are structurally heterozygous), or related to chromosome number (triploidy of the majority of cultivars leading to the formation of unbalanced gametes). Other phenomena that can be called genic lead to morphological and physiological abnormalities such as asynchronies or time lag in flower receptivity.

GENETIC RESOURCES

The species complex of bananas has characteristics that lend themselves to a particular method for genetic resource management. Clonal multiplication, associated with frequent sterility or incompatibility, and the coexistence of several levels of ploidy make it essential to have a profound understanding of the potentialities of each clone and of phylogenic relations between the different known types, to exploit the genetic resources for varietal improvement. Several tools have been developed for this purpose.

The major banana improvement programmes across the world have collections *ex situ*. Among the most important and best documented are those of the CARBAP (Centre africain de recherches sur bananiers et plantains) in Cameroon, IITA (International Institute of Tropical Agriculture) in Nigeria, FHIA (Fundación Hondureña de Investigación Agrícola) in Honduras, EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) in Brazil, MARDI (Malaysian Agricultural Research and Development Institute) in Malaysia, CRIH (Central Research Institute for Horticulture) in Indonesia, and CIRAD in Guadeloupe. These collections hold 300 to 500 clones each. Apart from conservation of the genetic patrimony, they serve as a basis and reference for varietal improvement. The objectives of the varietal creation programme associated with each collection determine the clones that are conserved *in vivo*. The collections of Cameroon, Nigeria, and Brazil are largely directed at local varieties for local consumption: Plantain in Africa, Pome and Silk in Brazil. The FHIA and CIRAD have larger collections, dedicated more to the improvement of export varieties. The CIRAD collection is particularly rich in diploid varieties related to the dessert types, material that is the basis for the procedure to create triploid hybrids developed in Guadeloupe.

On the international scale, INIBAP (International Network for the Improvement of Banana and Plantain) coordinates the different research programmes and mediates the exchange of certified material. INIBAP maintains in the name of the international community an *in vitro* collection of 1100 accessions at the international transit centre on the campus of the Catholic University of Leuven, in Belgium. It has also established two centres for indexing plant material to secure international exchanges, one at QDPI

(Queensland Department of Primary Industry) in Australia and the other at CIRAD in Montpellier, France.

Over the past twenty years, several markers of diversity have successively been perfected and applied to banana. Morphotaxonomic descriptors have been the primary markers developed and perfected in banana. Variations in vegetative organs occur mainly in the colour of the pseudostem, the presence and colour of blotches at the base of petioles, the shape of the petiolar canal section, and the size and shape of the plant. Particular variations are also recognized to be due to true dwarfism (shortening of plants, narrow leaves, shoot inhibition) and to chimeras of colour. The most significant variations are, however, those of the inflorescence and consequently the bunch. The size, shape, and colour of fruits as well as the colour of the pulp are among the criteria by which fruits are differentiated from one another. The Plantains, for example, have a very firm, yellow-orange pulp, which is not found in other cooking bananas such as Laknao, Popoulou, Bluggoe, and Monthan (Tezenas du Montcel, 1979). The bananas of East Africa are highly specific; they are intended for cooking or beer-making, depending on the clones. The fragrances of dessert bananas are varied, as well as their tastes: very sweet in certain diploid cultivars such as Pisang Mas, slightly acidulate in the Silk subgroup widely cultivated in India and Brazil, standard and generally agreeable for the Cavendish type meant for export. The morphological variability of the male bud is expressed partly by differences in the shape and colour of the bracts and the floral pieces.

A set of 119 agromorphotaxonomic descriptors has been defined as a norm of description for bananas (IPGRI-INIBAP and CIRAD, 1996). These descriptors serve as a basis for a system of information exchange between collections, the MGIS (Musa Germplasm Information System), run by INIBAP. Information tools have been developed to help identify plants on the basis of these descriptors (Perrier and Tezenas du Montcel, 1990).

The 119 descriptors were studied for 273 clones of the CIRAD collection and for 223 clones of the CRBP collection, 99 completely described clones being common to the two collections. The statistical analysis was done from an index of dissimilarity weighted for probabilities of observation error (see Appendix).

For ten years, different types of molecular markers have been used for banana (Lagoda et al., 1998): polyphenols (Horry, 1989), isozymes (Lebot et al., 1993), RFLP (Jarret and Litz, 1986; Carreel et al., 1994), and sequence tagged microsatellite sites (Grapin et al., 1998). Within CIRAD, these molecular data are grouped in the Tropgene database (Raboin and Lagoda, 1998). Other tools such as flow cytometry and *in situ* hybridization have also contributed to the characterization of genetic resources and allow a more refined determination of the genomic nature of the accessions studied: ploidy, aneuploidy, and number of chromosomes linked to each of the original species (Dolezel et al., 1994; Jenny et al., 1997; Horry et al., 1998; D'Hont et al., 1999).

The most complete results are related to the study of cytoplasmic and nuclear genomes with the help of RFLP markers.

The two cytoplasmic genomes are characterized by a single-parent heredity. Within the species *M. acuminata*, Faure et al. (1994) showed that the mitochondrial genome was transmitted by the paternal route and the chloroplast genome by the maternal. To date, all the monospecific and interspecific hybrids studied confirm this original transmission of cytoplasmic genome in banana.

The cytoplasmic and nuclear genomes of clones coming from the CIRAD collection at Guadeloupe and the *in vitro* collection of INIBAP were analysed by RFLP for 3 chloroplast probe-enzyme combinations, 14 mitochondrial probe-enzyme combinations, and 51 nuclear probe-enzyme combinations distributed throughout the genome. In total, 115 wild accessions and 243 cultivars were studied. Some 158 accessions, of which 89 are diploids comprising 34 wild species, and 69 are triploid, were compared with the morphological descriptions of the Guadeloupe collection. The list of clones studied having common morphological as well as molecular characteristics is presented in the appendix to this chapter (see Table 5).

From these successive inputs, the genetic resources of bananas were structured and their characterization was refined. This chapter presents a synthesis of those studies.

Diversity of Diploids

The diploid bananas, wild and cultivated, are presently much less widespread than the cultivated triploids. However, they are still found in the endemic state throughout Southeast Asia. The presence of seeds often makes the fruits unsuitable for consumption and sale. The plants are generally feeble and have smaller yields than the triploids. Only cultivars of the Sucrier type, which have small, very sweet fruits, are cultivated outside their zone of origin. These diploid clones are nevertheless indispensable for genetic improvement programmes, especially because of the high sterility of the triploids.

Wild bananas

The seminiferous wild bananas of the genus *Musa* are found in the humid but well-drained valleys and glades of forests at low and medium altitude, in the tropical zone, in South and Southeast Asia and in the Pacific, the Indian peninsula, and the Samoan islands. More than 25 species have been described and included within the genus *Musa*. Only those that have contributed to the genome of parthenocarpic bananas are discussed here.

Species belonging to the section *Australimusa* and *M. schizocarpa* of the section *Eumusa* are present east of the range of *Musa*: in the eastern area of Indonesia, Papua New Guinea, and the Pacific. The *Australimusa* are identified

by their erect inflorescence. The various species of this section were described by Cheesman (1947) and Argent (1976) as related and morphologically very close. The 16 accessions studied on the molecular scale are found to have little variation.

Musa schizocarpa is characterized by a water-green stem colour, identifiable in the interspecific hybrids, as well as the green colour of the bracts of the male bud. The two accessions studied and present in the collection are very similar from the morphological as well as molecular point of view.

Musa balbisiana, of the section *Eumusa*, is found in India, the Philippines, and occasionally the Indochina peninsula. The tree representation of morphotaxonomic data (Fig. 2), according to the NJtree method applied on the dissimilarity Δ_{pp}, clearly shows the differentiation of *M. balbisiana* in relation to *M. acuminata*, as well as their low variability (see Appendix). Isozyme analysis also reveals reduced polymorphism. Horry (1989) classifies the eight accessions present in the collection into four distinct types, which

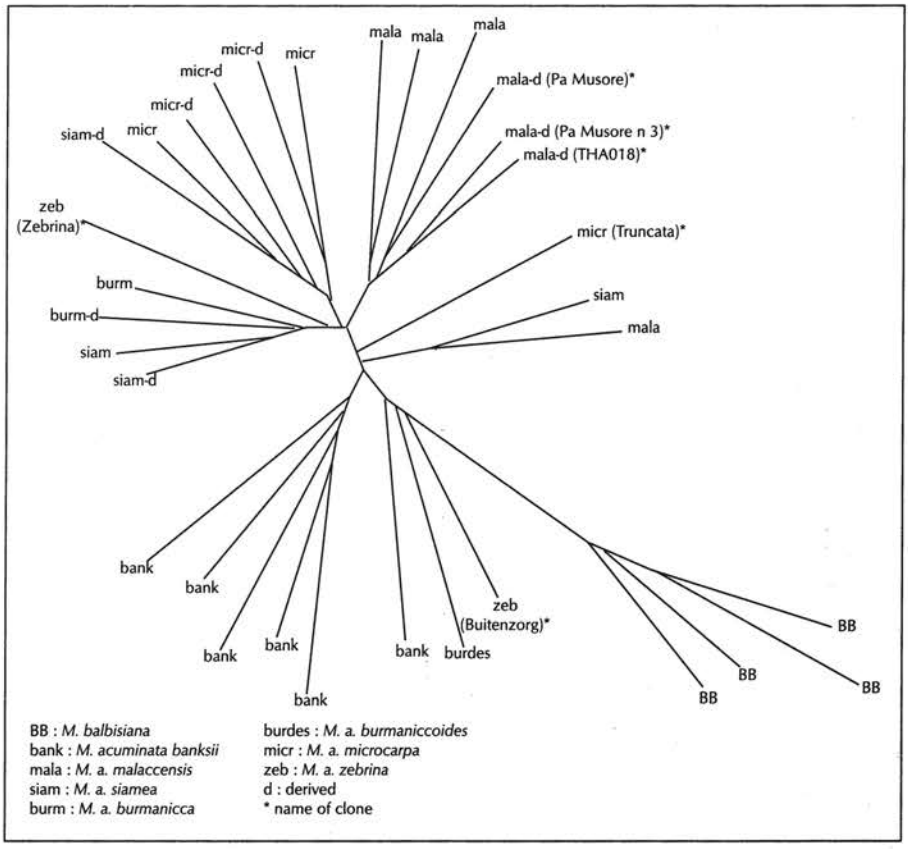

Fig. 2. Morphological diversity of seedy bananas (Guadeloupe collection): tree representation according to the NJtree method, realized on the Δ_{pp} of dissimilarity between 32 accessions on the basis of 99 morphological descriptors.

confirms the RFLP analysis. It is surprising that *M. balbisiana*, widespread over a vast geographic area, varies so little, but that could be due to lack of information.

The area of extension of *M. acuminata*, section *Eumusa*, covers most of the area of distribution of the genus *Musa*, from east to west, from Burma to New Guinea. Its botanical classification refers to 7 subspecies. The tree representation of the morphotaxonomic data spreads from four pools (Fig. 2), which correspond to *M. a. malaccensis*, *M. a. banksii*, and *M. a. microcarpa*, and to accessions of two subspecies, *M. a. siamea* and *M. a. burmanicca*. Nuclear RFLP analysis confirms these results and allows us to identify the intersubspecific nature of certain representatives of *M. acuminata*. Parallel analysis of two types of markers structures the species into five pools

The *M. a. banksii* pool constitutes a highly homogeneous set, more so in molecular terms than in morphological terms. Its representatives are highly autogamous and have diverged from other subspecies in an isolated fashion in Papua New Guinea. It is thus logical to observe that they are highly homozygous and morphologically original and related at the same time.

The *M. a. burmanicca* and *M. a. siamea* pool also comprises the subspecies *burmaniccoides*. These species originate from a vast continental zone from northern India to Thailand. Some very specific morphotaxonomic characters prevent the subspecies *burmanicca* and *burmaniccoides* from being grouped together, and de Langhe and Devreux (1960) therefore dissociated them. Analysis using molecular markers confirms the work of Shepherd (1990), who grouped them together.

The case of accessions of *M. a. zebrina* is a little peculiar: the Buitenzorg, heretofore considered the holotype, is highly atypical. The RFLP analysis proves its hybrid nature. It is not surprising, therefore, that these accessions are seen to diverge within the tree. The *zebrina* pool in the collection is made up of a single accession, Zebrina.

For the pool corresponding to *M. a. malaccensis*, it is necessary to introduce the notion of accessions derived from a subspecies. This appellation arises from the phenotypic observation of the accessions close to the holotypes, but not identical to them. These accessions (THA018, Pa Musore ..) are genetically identified as very close to the subspecies of origin by nuclear and cytoplasmic RFLP markers. They are more highly homozygous and are thus classified within the same group as *M. a. malaccensis*.

The same notion of derived accessions exists for *M. a. microcarpa*. The grouping is simple in morphological terms. Nevertheless, the accessions are polymorphic from the molecular point of view and RFLP analysis demonstrates their intersubspecific hybrid nature. It is nearly accepted that the accession Truncata, classified previously within *M. a. microcarpa*, constitutes an entire subspecies in morphological as well as molecular terms.

Musa acuminata is thus the most variable and best-structured species. The topography of its area of origin has led to geographic and thus repro-

ductive isolation, which is a source of differentiation. The chromosomal modifications of the translocation type observed by Shepherd (1987) between the subspecies of *M. acuminata* can be associated with this reproductive isolation.

Cultivated diploids

For the cultivated diploids, and despite the large number of clones known, no further subgroups have been established. Most of the cultivated diploid bananas present in the collection belong only to the species *M. acuminata*. Out of 135 diploid clones of the CIRAD collection, only about 10 accessions have been identified as interspecific and classified in the groups AB, AS, or AT, with the help of specific alleles of the species.

Factorial analysis on morphotaxonomic and molecular nuclear data reveals a nearly continuous cloud, and the structuration does not emerge. On the other hand, analysis of cytoplasmic genomes and rates of heterozygosity suggests elements of structuration.

The AA cultivars are separated into four of the nine chloroplastic profiles identified (designated I to IX) when all the *Musa* are analysed. Similarly, they present 47 of the 111 mitochondrial profiles identified. These last could be grouped into nine sets of clones having comparable mitochondrial profiles (designated α to ι). The AA cultivars are separated into five of these mitochondrial sets. Information on the chloroplast genome, indicating a maternal relationship, and that on the mitochondrial genome, indicating a paternal heredity, are complementary and can be compiled (Table 3). The AA cultivars can thus be divided into nine cytoplasmic types, or cytotypes, but most of them correspond to three cytotypes: II-α, V-α, or V-Φ.

The study of the nuclear genome has also made it possible to estimate the rate of heterozygosity using 43 probe-enzyme combinations that can be assimilated at loci, and thus appreciate the complexity of the genome and the intersubspecific or other origin of the clones. Two groups of clones can be distinguished within the three principal cytotypes. For example, within the V-φ, which comprise mainly clones from studies in Papua New Guinea, several clones have a low rate of heterozygosity (from 10% to 20%) and are closely related to *acuminata banksii*, in cytoplasmic as well as nuclear studies. The other cultivars have much higher rates of heterozygosity (40% to 70%), characteristic of an intersubspecific origin.

From the grouping into cytotypes and rates of heterozygosity, 12 sets of clones can be defined within the AA cultivars. This overall organization is found during nuclear genome analysis or morphological analysis. Nevertheless, the analyses show that the limits are somewhat arbitrary because the variation is continuous. From the classification, however, we can define the base populations for breeding programmes.

Table 3. Structuration of bananas according to their cytotype

Chloroplast profile	Mitochondrial profile								
	α	β	χ	δ	ε	ϕ	γ	η	τ
I									
II	*M. a. errans* AAcv (36)* AAA (Orotova, Red, Cavenish, Gros Michel) ABA (Mysore, Nadan, Pome)	AAcv (1)*	*M. a. burmanicca* *M. a. burmaniccoides* *M. a. siamea*	*M. a. malaccensis* AAcv (2)* AB ABA (Silk)	AAcv (1)*	AAcv (3)* AAA (3)**	*M. a. microcarpa*		ABB (Saba, Bluggoe, Ney, Mannan)
III	AAcv (4)* AAA (1)**				*M. a. malaccensis*				
IV	AAcv (1)*		*M. a. siamea*						
V	AAcv (49)* AAA (4)** ABA (Laknao, Maia Maoli) ABB (1)**				AAA (Lujugira-Mutika)	*M. a. banksii* AAcv (18)* ABA (Plantain, Popoulou, Laknao)		*ASs (2)**	ABB (Pelipita, Saba)
VI	AScv (1)*					*ASs (1)** AScv (2)*		*M. schizo-carpa*	
VII									*M. balbisiana* type 2
VIII	BAA (P. Rajah Bulu)				BAA (P. Kelat)				*M. balbisiana* type 1, 3, 4 BAB (Peyan, Saba, P. Awak)
IX									BAB (P. Awak)

*Number of clones having this cytotype. **Number of clones of indeterminate subgroup. In italics: seedy bananas. s: wild, cv: cultivated.

Triploid Bananas

Analysis on morphological data and molecular data has been done on triploid bananas (Fig. 3). The two types of markers clearly differentiate the triploid cultivars that are purely *acuminata* from interspecific cultivars. Simmonds and Shepherd (1955) based the classification of bananas into genomic groups

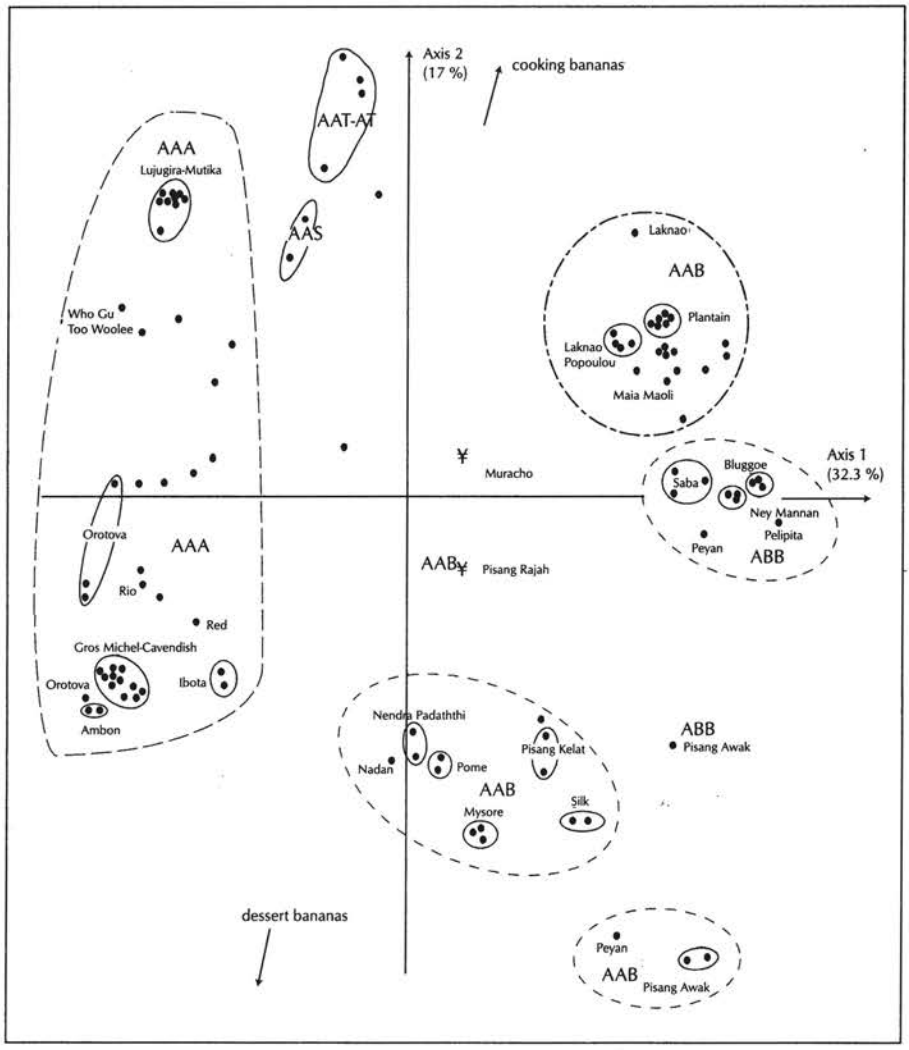

Fig. 3. Nuclear molecular diversity of triploid bananas according to their genomic group and subgroup. First plane of a factorial analysis on a Jaccard dissimilarity between 109 cultivars on the basis of 267 variables.

on the observation of 15 morphotaxonomic descriptors. The use of more complete descriptors and their analysis by multivariate statistical methods allow us to easily recover this organization in genomic groups, from observations from the Cameroon collection as well as the Guadeloupe collection.

On the other hand, the molecular data do not indicate as clear a distinction between AAB and ABB as morphological markers do. *Musa balbisiana* is found to be hardly polymorphic with the molecular markers, and the two genomes B of ABB are rarely differentiated. Several AAB cultivars also have their two A genomes nearly identical. In these two cases, the AAB and ABB clones have molecular profiles of the AB type, and only a reading of the relative intensity of RFLP bands—which is possible only for some probe-enzyme combinations—allows us to clearly differentiate the AAB from the ABB.

Although certain subgroups emerge from the morphological analysis, it is not always possible to identify the subgroups as easily as for Plantain or Cavendish. First of all, environmental variations strongly influence the stability of morphotaxonomic descriptors. Second, the mutations—themselves quite small—are the basis of the differentiation of cultivars within the subgroups causing phenotypic modifications (dwarfism, for example) that are strong enough to eliminate any hope of advanced structuring. In contrast, certain phenomena of convergence render illusory this type of analysis using only morphotaxonomic characters. One of the most glaring examples is probably the Mnalouki cultivar, AAB of the Comoro Islands, the appearance of which causes it to be mistaken for a Plantain of the French type: molecular markers and just a taste of the fruit, however, prove that it has nothing to do with the Plantain.

This botanical classification into subgroups is found more at the molecular level, the cultivars having identical or very similar nuclear and cytoplasmic profiles in most cases. The existence of some subgroups, such as the Orotova AAA, is nevertheless called into question. Certain clones that are not attached to any subgroup in morphological terms are somewhat related to each other, as with AAB Muracho, related to Pisang Rajah. Other clones that were earlier not grouped have been identified as closely related to each other, as with AA, Who Gu, and Too Woolee.

It is also possible to distinguish clones of the dessert type from clones of the cooking type within the AAB on a morphological basis, and within the three groups AAA, AAB, and ABB by means of molecular markers. Thus, among the AAB, bananas of the subgroups Mysore, Pome-Prata, and Pisang Kelat are differentiated from the typical cooking bananas: Plantain, Popoulou, Maia Maoli, and Laknao. It is to be noted that the clone Pisang Raja Bulu of the subgroup Pisang Rajah, of the mixed type, has a profile intermediate between the dessert and cooking types. This classification can be ascribed to the genome A of each of these subgroups.

The classification of triploid bananas is much easier to establish than that of the diploid clones because of the mode of evolution of the triploid clones. At this stage, all these cultivars are highly sterile and propagation is exclusively vegetative. The clones are differentiated among each other only through small mutations, which lead rapidly to the identification of true subgroups. The degree of variability within each subgroup depends on the intensity with which each type of clone will be used and thus multiplied. The greatest morphological variability is found in two subgroups particularly exploited in Africa: Plantains throughout the Central African zone and West Africa, and Lujugira in East Africa. On the other hand, within these subgroups, the nuclear and cytoplasmic RFLP profiles are identical or very similar.

Relationships between Different Levels of Variability

The crosses carried out during breeding involve clones of varying ploidy. The tetraploid hybrids are a result of crosses between the triploid cultivar to be improved and a diploid progenitor that carries resistance. The procedure developed by CIRAD aims to produce triploid cultivars related to cultivated varieties from diploid progenitors (Bakry et al., 1997). In these two situations, a thorough knowledge of the origin of cultivated bananas is essential. An understanding of the processes of domestication—parthenocarpy, sterility, and evolution towards triploidy—is also necessary to best manage and exploit the genetic resources of banana. Through the study of the genetic organization of bananas, we try to identify populations of present diploids most closely related to different types of triploid cultivars.

Several morphological resemblances are known between diploid and triploid clones. The bunches of several AA cultivars—Pongani, for example—that come from collections in Papua New Guinea are similar to those of the Plantains. The taste and type of consumption of other AA cultivars, such as IDN110, relate them to triploids of the Silk type. These relationships have been confirmed by molecular analysis of cytoplasmic and nuclear genomes, and other relationships have been brought to the fore.

The analysis of cytoplasmic genomes, presented for the cultivated diploid clones, has been extended to all the wild and cultivated clones, diploid or triploid. In Table 3, two clones shown on the same line are related from the maternal side and two clones in the same column are related on the paternal side, independent of their level of ploidy. Many triploids are of the same cytoplasmic group as wild or cultivated diploids. Thus, cultivars of the subgroups Cavendish, Gros Michel, Ambon, Rio, and Ibota have the same cytoplasmic profiles as several AA cultivars. AAB clones of the dessert type in the Silk subgroup have the same cytoplasmic profile as the AB of the Silk type. AAB clones of the cooking type in the subgroups Plantain, Popoulou, and Laknao have two cytoplasmic genomes identical to that of *M. a. banksii*. This relationship between the two genomes A of Plantain and *M. a. banksii*

has been revealed by morphological observations (Tezenas du Moncel, 1990). It has been confirmed by genome analysis with isozymes (Horry, 1989) as well as by RFLP marking. For three subgroups of triploids, no diploid clone belongs to the same cytoplasmic group or to the same mitochondrial profile. Among them, the AAA clones of East Africa, which belong to the subgroup Lujugira-Mutika, belong on the maternal side to *M. a. banksii* and on the paternal side to *M. a. zebrina*, which demonstrates an intersubspecific origin, confirmed by the analysis of their nuclear genome. This bisubspecific origin has also been found for the AA cultivars of nearby geographic origin, of Madagascar or the Comoro Islands.

The set of clones has also been analysed with the same nuclear RFLP markers. The projection of data on cultivated triploids on the results obtained for *M. acuminata* and the cultivated diploids reveals the relationships between the A genomes of wild clones, cultivated diploids, and triploids (Fig. 4). It is interesting to observe that the diploid and triploid cultivars of the sets related

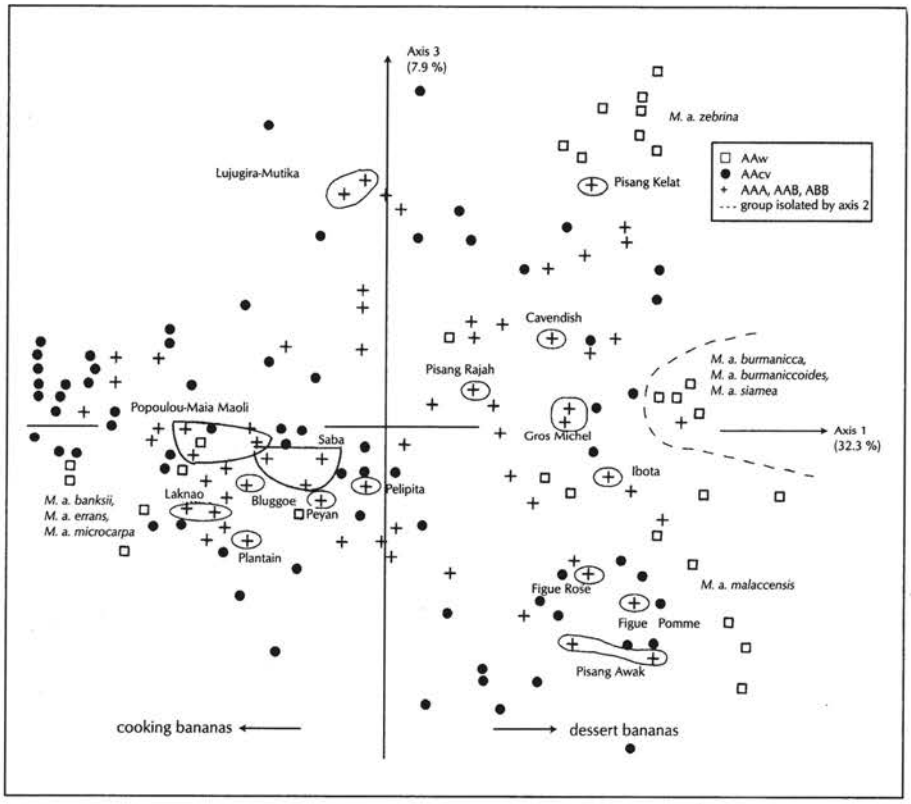

Fig. 4. Nuclear molecular relationship between the A genomes of triploid bananas and that of the wild and cultivated diploids: projection of data relative to triploids on the 1-3 plane of the factorial analysis on a Jaccard dissimilarity of wild and cultivated diploids on the basis of 19 probe-enzyme combinations that reveal significant differences between the cytotypes V-α and V-Φ

to the *banksii, errans,* and *microcarpa* Borneo axes have floury fruits and are thus consumed cooked, while bananas of the groups close to the *malaccensis* and *zebrina* axes have sweeter fruits.

The study of nuclear genome has also been used to estimate the rates of heterozygosity from a profile at two levels of bands, for the set of clones, and a profile at three levels of bands, for the triploids, using 43 probe-enzyme combinations that can be assimilated at loci. These rates allow us to assess the complexity of the genome of triploids to be improved. The different A genomes of a single genotype are more related—their rates of heterozygosity lower—for the cooking types than for the dessert types, which thus have a more complex origin.

The cytoplasmic and nuclear data on diploids and triploids allow us to target the diploid progenitors most closely related to the triploids to be improved. Thus, on the basis of molecular markers, crossing procedures of diploids to be improved, doubled with colchicine or not, have been established in order to obtain hybrids similar to the triploids, such as those that were proposed by Raboin et al. (forthcoming) for Gros Michel and Cavendish.

CONCLUSION

From all the morphological and molecular data, hypotheses have been advanced as to the origin of parthenocarpy and principal subgroups of triploids.

Dispersal and Evolution of Banana

Simmonds (1962) placed the centre of primary domestication of cultivated bananas in the Malaysian region. However, several results suggest that it is the genomes of *M. a. banksii* accessions of Papua New Guinea and the accession Agutay of the Philippines, representing *M. a. errans,* that are the origin of parthenocarpy and thus of cultivated bananas. The nuclear or cytoplasmic genomes of these two subspecies have been identified in almost all the parthenocarpic bananas, diploid or triploid. Moreover, the genetic distances are minimal between *M. a. banksii* and the homozygous AA cultivars. Simmonds (1962) indicated moreover a significant development of the pulp, which is an index of parthenocarpy, in a representative of the subspecies *banksii*. The Philippines and Papua New Guinea area, where the two subspecies *banksii* and *errans* originated, thus seems to be the centre of primary domestication.

The fruits of certain wild bananas are consumed immature before the seeds become hard. The *M. a. banksii,* which presented the beginning of parthenocarpy, were selected by humans. Transported to Southeast Asia, they were crossed with other subspecies of *M. acuminata* and thus acquired the genetic and structural heterozygosity that characterize all the cultivars. They

integrated genes of sterility and regulatory genes of parthenocarpy to give the first edible diploids. For these diploids, the sterility of cultivars limited the occurrence of a panmictic unity in each region and vegetative propagation conserved the intermediate forms. Thus, despite geographic isolation, no strong structuration appeared. The partial fertility of these cultivars has nevertheless, gradually and under human action, allowed the establishment of a cline. Vegetative propagation allowed the genotypes resulting from each of these steps to be conserved.

The AAB Plantains, present in the entire forest zone of Africa (Champion, 1967), were introduced in ancient times on that continent. The introduction had an Austronesian origin and dated from at least 3000 years BCE (de Langhe, 1995). Champion notes that it took place at a time when other bananas did not exist, otherwise those also would have been introduced into Africa. These bananas, like the Popoulou, also called Pacific Plantain, have their two A genomes very closely related to that of *M. a. banksii* and do not belong to any other subspecies. The parthenocarpic bananas of the subspecies *banksii* could have been crossed with *M. balbisiana* in areas covered by the two species. The genomic differences between *M. a. banksii* and *M. balbisiana* are sufficient for their hybrids to give diploid gametes resulting from a single restoration. The AAB derived from these few crosses expanded towards the west, into India and then Africa, where they were differentiated and propagated. Central Africa is thus the centre of secondary diversification of Plantains. The crosses between AA of *banksii* origin and *M. balbisiana* have also led to Laknao in the Philippines, and Popoulou-Maia Maoli in the Pacific.

The Lujugira-Mutika AAA were not observed in East Africa. They are related to the two subspecies *banksii* and *zebrina*. These clones or the diploids from which they were derived were introduced directly from Indonesia, the zone of origin of *M. a. zebrina*, perhaps via the Comoro Islands and Tanzania, as Simmonds has hypothesized. Transported to Indonesia by the Austronesians, the partly parthenocarpic bananas of *banksii* coming from Papua New Guinea could have been crossed with *M. a. zebrina*. Since the hybrids were structurally heterozygous, their partial sterility was sufficient to give diploid gametes required for the formation of triploids.

The formation of triploid cultivars of the dessert type relies on the existence of hybrid cultivars between the *banksii*, *errans*, *malaccensis*, and *zebrina* genomes. Diploid and then triploid cultivars that relate these genomes appeared progressively in Malaysia. This region is thus, according to our hypothesis, a secondary centre of domestication and not, as Simmonds has proposed, the primary centre.

Conservation of Genetic Resources

The collected cultivated clones—about a thousand, which is a small number compared to that of other plants—are conserved *in vitro* and managed by

INIBAP. Each research centre maintains an *in vivo* collection of clones representative of the diversity and several clones corresponding to the type of fruit the centre wishes to improve. In the natural environment, the variability is mostly of somaclonal origin because of the high sterility of cultivars. The variability resulting from recombination arises essentially from artificial crosses carried out during the creation of a variety. By characterizing the created clones accurately, and comparing that characterization with that of clones of natural origin, we can verify that there is no genetic drift.

The situation is entirely different for the seminiferous bananas. Several species and subspecies of the genus *Musa*, which have been studied very little, are represented in the collection only as holotypes that are maintained by vegetative propagation. These varieties are difficult to study owing to the geographic and political situation of their countries of origin, but it is essential to study them because of the accelerated deforestation of the zones they grow in. A number of wild populations are at risk of extinction in the short or long term. The conservation and knowledge of these varieties are essential for future improvement programmes, which look for new sources of resistance to parasitic threats.

APPENDIX

Choice of a Distance for the Analysis of Morphotaxonomic Descriptors

One of the characteristics of morphotaxonomic descriptors is their subjectivity. The choice of a modality depends on the expression of the character in the plant as a function of the environment and on the researcher's evaluation of this expression. Despite all efforts to reduce this subjectivity, it is impossible to eliminate it completely. The variations of expression, however, constitute one means of access to the plant's responses to its environment. A particular dissimilarity has been defined, taking into account these errors of evaluation.

Definition of the Dissimilarity Δ_{PP}

The descriptors retained are qualitative. In order to refine the responses, a matrix of probability of error has been associated with each descriptor. In the Musaid software (Perrier and Tezenas du Montcel, 1990), the use of these probabilities means we do not have to systematically consider that two accessions are the same or not but rather we can assign a weight to their similarity. In Table 4, for example, in which the colour of the ventral face of the midrib is recorded, the notation 'light green' can easily be confused with 'yellow' or 'green', while the notation 'black' is unequivocal.

Table 4. Matrix of probability for the descriptor 'colour of ventral face of the midrib'

Response	Probability of identity					
1—yellow	43	30	10	05	01	01
2—light green	30	33	30	05	01	01
3—green	20	30	53	05	01	01
4—pink purple	05	05	05	64	10	01
5—red purple	01	01	01	01	86	01
6—black	01	01	01	01	01	95

The index of dissimilarity defined derives from the Sokal and Michener index (or simple matching coefficient, designated Δ_{SM}), which, for two accessions, is equal to the ratio of the number of equal responses to the number of descriptors compared. Here our index, written Δ_{PP}, is weighted by the probabilities of error of observation. The contribution of the descriptor v to the dissimilarity between two accessions i and j is expressed as follows:

$$\Delta_V = \frac{1}{2}\left[\frac{P_v(v_i, v_i) - P_v(v_i + v_j)}{P_v(v_i, v_i) - P_v(v_i + v_j)} + \frac{P_v(v_j, v_j) - P_v(v_j + v_i)}{P_v(v_j, v_j) - P_v(v_j + v_j)}\right]$$

where P_v represents the matrix of probability associated with the descriptor v and where v_i and v_j correspond to the responses of two accessions for this descriptor. The overall dissimilarity Δ_{PP} between i and j is equal to the mean of Δ_V over all the descriptors.

For a descriptor, Δ_V varies between 0 and 1, it is null when the two individuals have the same modality and large to the extent that the probabilities attached to the responses v_i and v_j are different, without, however, reaching 1.

Thus, for the descriptor of the colour of the ventral face of the midrib, we obtain, if $v_i = 2$ (light green) and $v_j = 3$ (green):

$$\Delta_{PP} = \frac{1}{2}\left(\frac{33 - 30}{33 + 30} + \frac{53 - 30}{53 + 30}\right) = 0.16$$

If $v_i = 2$ (light green) and $v_j = 6$ (black):

$$\Delta_{PP} = \frac{1}{2}\left(\frac{33 - 1}{33 + 1} + \frac{95 - 1}{95 + 1}\right) = 0.96$$

In these two situations, the index Δ_{SM} would be equal to 1.

The index Δ_{PP} tends to minimize the differences observed between accessions. It offers the advantage of preventing an excessive increase of the index calculated by accumulation of minor differences between morpho-taxonomic criteria that are difficult to evaluate. This gain in precision for small distances is a desired advantage, since small distances have a great importance in the first state of ascending algorithms of classification.

The graphic representation of Δ_{PP} as a function of Δ_{SM} indicates that the linear correlation between the indexes is good ($r = 0.896$). The two indexes have a clear tendency to measure the divergences between accessions in the same direction. The extreme points are the same, but the values in the middle are divided by a factor of about 2 with the index Δ_{PP}.

Comparison of the Index Δ_{PP} in the Various Collections

For this analysis the official descriptors of bananas (IPGRI-INIBAP and CIRAD, 1996) were used. The observations were made on two collections, in Cameroon (CRBP) and Guadeloupe (CIRAD). Only the bananas for which the descriptors were complete in the two collections were used. Thus, 99 accessions were retained: 58 diploids and 41 triploids.

The means of the Δ_{PP} indexes were calculated for each collection and for each genomic group. Observation of the same cultivars on the two sites allows us to quantify and distinguish the variability observed between different cultivars within a single collection from the variability between collections

for the same cultivar. The comparison of results allows us to highlight some main points.

There is less divergence between sites than between cultivars for the collections in general and, more precisely, for the AAA and AAB groups. On these scales of diversity, the environmental effects do not disturb the classification of clones in the genomic group. On the other hand, the divergence becomes higher for the subgroups. For a subgroup in which homogeneity between cultivars is large, variations linked to the environment have more influence than the differences between clones. This is the case of Cavendish, which differ among themselves essentially in often minute variations of size. The influence of the environment on these variations is high, and the divergence will be larger between descriptions of the Grande Naine clone at Cameroon and at Guadeloupe than between the description of a Grande Naine and that of a Williams in a single collection. Since the clones respond in the same way to the influence of the environment, the variation within a single site is possibly displaced, but it is not amplified.

The Δ_{PP} index, which takes possible errors into account using tables of probabilities, allows a more reliable determination of the Δ_{SM} index genomic group than even when data from another collection is used. On the other hand, to identify a cultivar, it is not always reliable to use a reference base (Cameroon, for example) to determine an accession described in another geographical area (Guadeloupe, for example), especially when there are accessions resulting from somaclonal mutations. This confirms the recommendations to use a probability model (Musaid software) to identify an accession.

Table 5. List of clones studied having common morphological as well as molecular characteristics

Section ● Group species	Subgroup Subspecies	Clone Variety	GLP CMR*	 RFLP**
Rhodochlamys				
● *Musa velutina*		Velutina	x	x
● *Musa laterita*		Jamaïque		x
Eumusa				
● *Musa acuminata*	*malaccensis*	Pahang, Sélangor	x	x
		Cici (Brazil), Malaccensis		x
	burmanicca	Long Tavoy		x
	burmaniccoides	Calcutta 4	x	x
	banksii	Banksii, Madang, Paliama	x	x
		Hawain 2, Higa, Waigu		x
	siamea	Khae (Phrae), Pa Rayong	x	x
	microcarpa	Bornéo, Microcarpa, Truncata	x	x
	zebrina	Zebrina	x	x
		Burtenzorg		x

(Contd.)

(Contd.)

Section • Group species	Subgroup Subspecies	Clone Variety	GLP CMR*	 RFLP**
	malaccensis derivative	Pa (Musore) n° 3, THA0l8	x	x
		Pa (Musore)		x
	burmanicca derivative	Pisang Prentel		x
	siamea derivative	Pa (Songhkla)	x	x
		Pa (Abyssinea)		x
	microcarpa derivative	Pisang Cici Alas	x	x
		AAs IDO113, EN13		x
• *Musa balbisiana*		Balbisiana (CMR), Balbisiana (HND), Klue Tani, Pisang Batu	x	x
• Cultivated AA		Akondro Mainty, Ato, Bie Yeng, Chicame, Galeo, Gorop, Guyod, IDN110, Kenar, Khai Nai On, Kirun, M48, M53, Manameg Red, Mapua, Niyarma Yik, Pa (Patthalong), Pisang Bangkahulu, Pisang Berlin, Pisang Sasi, pongani, Sa, Samba, Sepi, SF215, SF265, Sowmuk, Thong Det, Tomolo, To'o, Tuu Gia, Vudu Papua, Wikago	x	x
		Bebeck, Beram, Dibit, Fako Fako, Gu Nin Chiao, Hom, Inori, Khi Maeo, Kumburgh (Kunburg), Manang, N° 110-THA052, Padri, Pallen Berry, Pisang Gigi Buaya, Pisang Lilin, Pisang Sapon, Pitu, Saing Todloh, Ta, Wudi Yali Yalua		x
• Cultivated AB		Figue Pomme (Ekona), Safet Vetchi	x	x
		Kunnan		x
• AAA	Gros Michel	Cocos, Gros Michel	x	x
		Bout Rond, Dougoufoui, Highgate		x
	Cavendish	Americani, Mutant Rouge, Padji, Seredou	x	
		Grande Naine, Petite Naine, Poyo	x	x
		IRFA901 Williams		x
	Red/Green Red	Figue Rose Naine		x
	Orotova	Pisang Sri	x	x
		Hom (Sakhon Nakhon), Orotova, Pisang Kayu, Pisang Umbuk		x
	Ibota	Khom Bao, Yangambi km5	x	x
	Lujugira	Foulah	x	x
		Bui Se Ed, Nakitengwa, Nshika		x
	Ambon	Hom (Thong Mokho), Pisang Ambon, Pisang Bakar		x
	Indeterminate AAA	Ouro Mel, Too Woolee Who Gu	x	x

(Contd.)

(Contd.)

Section • Group species	Subgroup Subspecies	Clone variety	GLP CMR*	GLP RFLP**
		Lagun Vunalir, Palang		x
• AAB	Plantain	Amou, Kelong Mekintu, Kwa,	x	
		Madre del Platano	x	
		Big Ebanga		x
	Pisang Kelat	Pisang Kelat, Pisang Pulut		x
	Pisang Rajah	Pisang Raja Bulu	x	x
	Popoulou	Poingo, Popoulou (CIV)		x
	Nendra Padaththi	Pisang Rajah	x	x
		Rajapuri India		x
	Mysore	Pisang Ceylan	x	x
	Silk	Kingala 1, Supari	x	
		Figue Pomme Naine		x
	Nadan	Lady Finger		x
	Pome	Guindy, Rois	x	
		Foconah, Prata Ana		x
	Laknao	Laknao	x	x
		Kune, Mugus		x
	Indeterminate AAB	Mnalouki	x	
		Pisang Nangka	x	x
		Kupulik, Muracho, Teeb Kum, Tomnam	x	
• ABB	Bluggoe	Dole, Poteau Nain	x	
	Pisang Awak	Bom, Praha	x	
		Namwa Knom, Pisang Kepok		x
	Monthan	Monthan	x	x
	Ney Mannan	Ice Cream	x	x
		Radjah		x
	Peyan	Brazza IV, Pisang Kepok Bung		x
	Saba	IDN107		x
		Saba	x	x
	Indeterminate ABB	Auko-PNG034, Dwarf Kalapua	x	x
		Auko-PNG125, Klue Tiparot***		x
• AAAA		Champa Nasik	x	
• AAAB		Langka 08	x	x
		Ouro da Mata, Platina	x	
• AABB		Pisang Slendang		x
• ABBT		Yawa 2		x
Total			99	158
		cultivated diploids	37	55
		wild diploids	21	34
		triploids and tetraploids	41	69

*Population common to the Guadeloupe and Cameroon collections, morphotaxonomic descriptors.
**Accessions of Guadeloupe described by RFLP markers as well as by morphotaxonomic descriptors.
***New classification, according to Jenny et al. (1997).

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